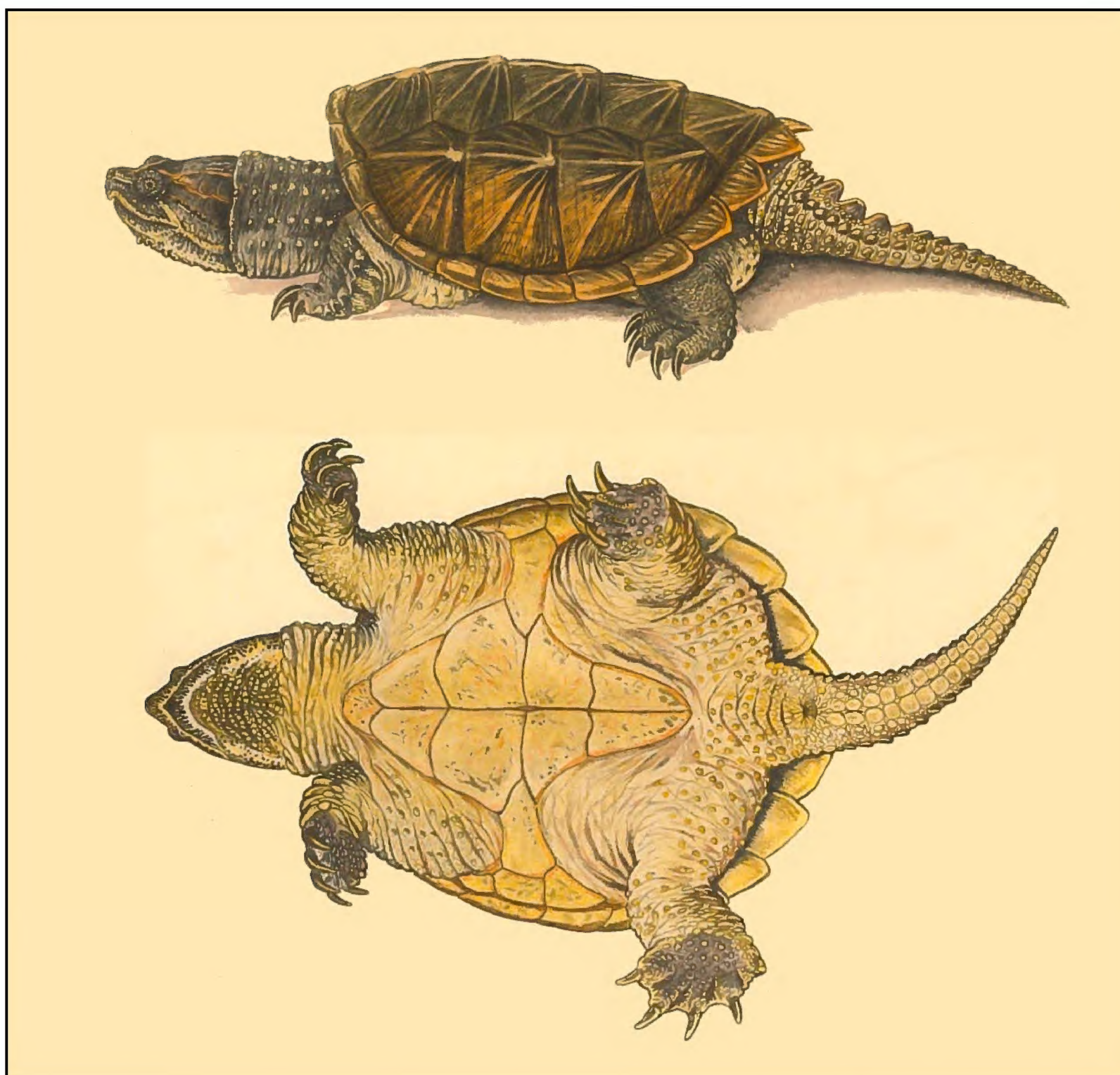

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An Overview of the Paleoclimatic Influences on the Genetic Variation of *Chelydra*

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Abstract

Prior research on the North American turtle species, *Chelydra serpentina* (North American Snapping Turtle), has produced an unanticipated observation. There is low variability in the normally hypervariable displacement loop (d-loop) of the control region mitochondrial DNA (CR mtDNA). Paleoclimatic data was used to qualitatively investigate the causes for the lack of genetic variation observed in *C. serpentina*. For comparison, similar investigations were made on the ranges of two understudied related species, *Chelydra rossignonii* (Mexican Snapping Turtle) and *Chelydra acutirostris* (South American Snapping Turtle). A series of Pleistocene bottlenecks caused by a southward climatic shift in the 18°C mean July temperature (apparently needed for egg incubation) and lethal marine transgressions over the Florida Peninsula related to interglacial transitions offer an explanation for the low genetic diversity of CR mtDNA found among *C. serpentina* populations. In contrast, the Central and South American species both have Pleistocene glacial-interglacial refugia embedded within significant portions of their ranges. These climatically stable regions isolated the two species and promoted genetic divergence.

Foreword

This overview attempts to combine for the genus *Chelydra* two disparate fields: paleoclimatic studies and population genetics. In the tradition of a synthesis paper, associations between established disjunctive data sets are made which the authors believe have not been firmly or previously presented. Since the subject of this investigation is based on the succession of geological events and is somewhat historical in nature, this paper will be appropriately presented in a narrative format. A series of glaciations are proposed to have caused population bottlenecks within the North American species. These continental and peninsular reductions in the range of *Chelydra serpentina* combined with the uniquely high mobility of this species caused the lack of polymorphism observed in the control region mitochondrial DNA (CR mtDNA), which is generally not observed in other less mobile species of North American turtles.

Introduction

Two genera of highly aquatic turtles endemic to the Americas are found in the family Chelydridae: three species of the genus *Macrochelys* (Alligator Snapping Turtle) and three species of the genus *Chelydra* (Snapping Turtle). Although fossil relatives have been found in Eurasia, the ancestral center of origin for Chelydridae is in North America (Hutchison, 2008). The oldest fossil records of *Macrochelys* and *Chelydra* date from the early Miocene 19 Ma (Mega-annum, or millions of years before the present) and the middle Miocene 16.5 to 11.5 Ma, respectively (Holman and Sullivan, 1981; Hutchison, 2008). It is unclear where in North America *Chelydra* originated, *Chelydra*-like fossils that date from the Late Paleocene about 56 Ma have been found in the Pacific drainage, suggesting possible origin west of the Rocky Mountains (Hutchison, 2008). Conveniently, 56 Ma the Paleocene-Eocene Thermal Maximum (PETM) also occurred. The onset of this horizon event was an

anomalous greenhouse spike that caused global environmental stresses which selected for phenotype frequency shifts favorable toward genetic assimilation leading to speciation. The near arctic had a Carolinas-like climate and as a consequence of this hothouse world the continental shorelines were altered by a 67 m sea-level rise that flooded the Mississippi basin into an expansive marine bay (Kunzig, 2011; Bowen and Zachos, 2010). This rapid climatic change formed a relatively short term intense episodic and selective speciation event that established an array of several orders of mammals such as primates and ungulates, lending some basis for a western establishment of the genus *Chelydra*. Other older fossil evidence, however, suggests the likely ancestral range of *Chelydra* (*Protochelydra*) is east of the Rocky Mountains (PETM may have provided favorable climate that expanded the distribution of *Chelydra*) about 57 Ma (Ernst and Barbour, 1989; Steyermark et al., 2008). This is further supported by the geographical overlap of the region with the largest range of the oldest extant species, *Chelydra serpentina*, while no species of *Chelydra* currently range in the Pacific drainages (Phillips et al., 1996). Recently three extant species of *Macrochelys* have been recognized (Thomas et al., 2014): *M. temminckii* (Mississippi river drainage), *M. apalachicola* (Apalachicola river drainage), and *M. suwanniensis* (Suwannee river drainage). The current range of *Macrochelys* is restricted to the southern United States east of the Rocky Mountains notably excluding the Florida Peninsula and Atlantic coastal plain. Two extinct species of the genus are recognized, *M. schmidt* from the early middle Miocene of Nebraska and *M. auffenbergi* from the middle Pliocene of Florida (Auffenberg, 1957; Lovich, 1993). In contrast, the extensive range of *Chelydra* (from 51°N to 2°S latitude) over diverse geographic and climatic regions (Figure 1) has provided conditions favorable for both intraspecific and interspecific morphological diversity.

Interpretation of the taxonomic diversity of the genus *Chelydra*

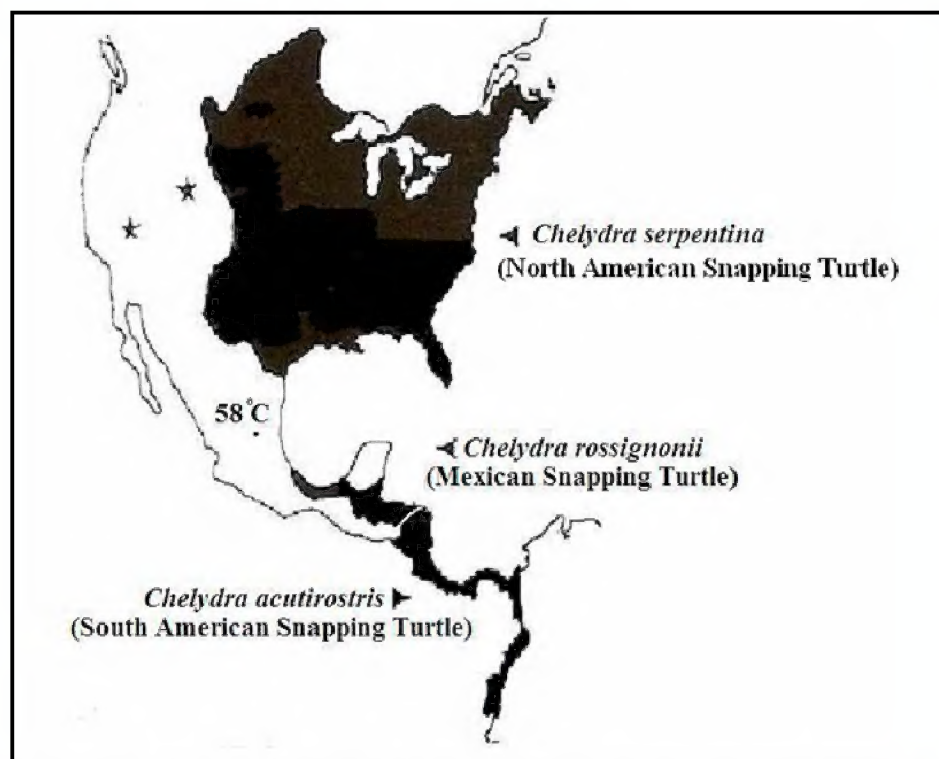


Figure 1. The distribution of *Chelydra serpentina*, *C. rossignonii* and *C. acutirostris* across the Americas (modified from Gibbons et al., 1988). The two stars mark the locations of fossil specimens (presumably *C. serpentina*) found west of the North American continental divide in Nevada and Idaho, evidence of a more extensive range. Note the range gap in northeastern Mexico where a temperature of 58°C (136°F) was recorded (Bartholomew et al., 1980), indicative of an extremely arid inhospitable barrier region for *Chelydra* terrestrial migrations.

has ranged from monospecific taxonomy with no subspecies (Carr, 1952) to one species with an inflated four subspecies (Feuer, 1966; Gibbons et al., 1988; Pritchard, 1989). Current taxonomic consensus, however is more speciose, recognizing one North American species (no subspecies) and two species found in Central and South America (Shaffer et al., 2008). The range of *C. serpentina* (North American Snapping Turtle) extends westward more than 2500 km inland from the Atlantic coast of the United States, the largest range of any species of *Chelydra*. One early researcher impressed with the range of the genus, more than 7000 km from northeast to southwest, remarked, “this species furnishes a case of distribution unparalleled among reptiles, ranging as it does from the (nearctic) cold regions of Canada to the torrid region of Ecuador” (Cope, 1868).

The distribution of *Chelydra rossignonii* (Mexican Snapping Turtle) ranges from the Gulf coast lowlands of southern Mexico’s Tabasco Plain (bordered in the east by the Tuxtla Mountains) and proceeds along the southern lowlands at the base of the Yucatan Peninsula to eastern Honduras (Gibbons et al., 1988). The range of *C. rossignonii* is separated from the range of *C. serpentina* in North America by more than 800 km across northeastern Mexico and is also adjacent to the range of *Chelydra acutirostris* (South American Snapping Turtle). This third species of *Chelydra* ranges southward from Honduras to the northern coast of Ecuador.

The disparity between the widespread range size of *C. serpentina* and those of other species of *Chelydra* demonstrate two biogeographic concepts. The range of *C. serpentina* follows Rapoport’s Rule: organisms in northern latitudes have characteristically wider latitudinal ranges compared to those in low latitudinal tropical regions (Rapoport, 1982). Seasonal climatic fluctuations of temperate regions select for populations with tolerances for the variety of habitats inherently found over such large ranges. In contrast, the smaller ranges of *C. rossignonii*

and *C. acutirostris* demonstrate distance decay: Another biogeographic concept that explains the small ranges and consequent high species densities characteristically found in the tropics creating diversity hotspots (Nekola and White, 1999).

Background

A study conducted on *C. serpentina* in ten states of the southern United States from 20 drainage systems indicated no genetic structure with virtually no variation in the CR mtDNA sequence (GenBank accession number: AF029986.1) within the species (Walker, Moler et al., 1998). Five *C. serpentina* captured in the Mississippi Delta and one in South Carolina had different CR mtDNA haplotypes. Combined they made up a minority (9.1%) of the total number of turtles studied ($n = 66$). Monomorphic haplotypes are by one definition found in 95% (conservatively 100%) of the sample population (Halliburton, 2004). As the monomorphism in the North American species was approximately 91% of the sampled population (Walker, Moler et al., 1998), the morphotype is technically not monomorphic; therefore, hereafter the major haplotype will be referred to as the predominant CR mtDNA haplotype (rather than monomorphic haplotype). In a more recent study, the lack of genetic diversity was confirmed from more representative samples ($n = 50$) taken from 20 states. Two polymorphic pockets were found in Arkansas and Indiana (Shaffer et al., 2008). The Florida Peninsula population has traditionally been classified as a subspecies based on distinct morphological characteristics (Feuer, 1966); however, the CR mtDNA of this population has no variation from the predominant CR mtDNA haplotype of continental *C. serpentina*, so at the moment the two populations cannot be distinguished based solely on CR mtDNA sequence analysis and are currently taxonomically classified as one species with no subspecies.

The lack of structure in the sequence variation of CR mtDNA for as much as 1000 km across southern range of *C. serpentina* suggests this species has a propensity for a deme of one predominant CR mtDNA haplotype. In contrast, *Macrochelys*, which also ranges across the southern United States, has three major haplotypes (recently identified as full species; Thomas et al., 2014) with up to 11 minor haplotypes (Roman, 1997). Members of the family Kinosternidae (musk and mud turtles) and other genera of turtles in the same region also display greater genetic variation (Walker and Avise, 1998; Walker, Orti and Avise, 1998; Serb et al., 2001). The low genetic diversity of *C. serpentina* is reminiscent of the genetic research on the highly mobile (high mobility of a species is suspected to be a key behavioral trait contributing to genetic monomorphism) *Acinonyx jubatus* (East African Cheetah) which has at least two haplotypes, one major population located in sub-Saharan East Africa, *A. j. raineyi*, that experienced a population bottleneck — probably in the latest Pleistocene / earliest Holocene 10 ka (thousand years ago) and a second minor population found in South Africa, *A. j. jubatus*, thought to have been isolated about 100 years ago (O’Brian et al., 1987).

The first major study on the genetics of all species of *Chelydra* used Amplified Fragment Length Polymorphism analysis (AFLP: Phillips et al., 1996). The advantage of this molecular

diagnostic technique is that it analyzes longer DNA sequences (the entire mitochondrial plasmid compared to DNA sequence analysis of roughly 500 bp at a time). It is debatable whether AFLP analysis is as informative as CR mtDNA sequencing, but previous work on *Sternotherus minor* (Loggerhead Musk Turtle) has shown this type of fragment length analysis provides data that result in similar conclusions (Walker et al., 1995). The estimated percent sequence divergence of mtDNA between *C. serpentina* ranged between 0.1% and 0.5% with a minority having no variation. Generally the estimated sequence variation of mtDNA within the North American species was extremely low, in agreement with Walker, Moler et al. (1998). The estimated percent sequence divergence of mtDNA between *C. serpentina* and *C. rossignonii* specimens was as high as 5.6%. The genetic variation of mtDNA among two Veracruz *C. rossignonii* specimens was 0.9 %. The estimated sequence divergence of mtDNA between two *C. acutirostris* from Esmeraldas, Ecuador, was 0.6% while the greatest estimated sequence divergence between *C. acutirostris* and the North American species was 4.3%. The mtDNA sequence divergence between *C. rossignonii* and *C. acutirostris* was 2.6%. Based on these observations, Phillips et al. (1996) suggested that *C. rossignonii* and *C. acutirostris* have different haplotypes than the North American subspecies, and, albeit both were based on one comparison, have polymorphic CR mtDNA. Preliminary results from another study using the same *C. rossignonii* tissue samples as Phillips et al. (1996), and a third from Honduras (based on the sequence analysis of CR mtDNA as in the Walker study, actual sequences not listed in manuscript) confirm that these sequences are polymorphic (Shaffer et al., 2008).

Phillips et al. (1996) estimated from their data that ancestral *C. rossignonii* populations became established and diverged from the two North American subspecies 11.12 to 22.25 Ma. The earliest record of *Chelydra* is from the type section of the Valentine Formation of Nebraska considered to be Barstovian in age, ca 16.5 to 11.5 Ma (Holman and Sullivan, 1981). This suggests the dispersal of *Chelydra* into the vacant habitats of Central America and its subsequent speciation occurred soon after the appearance of the genus. This dispersal event coincided with the end of the Miocene when permanent arctic icecaps formed (de Blij, 2005). Paleoclimate data fits the time period Phillips et al. found for the separation of *Chelydra* populations in Central America and consequent *C. rossignonii* speciation. About 15–13 Ma, oceanic paleothermohaline currents were altered by driving tectonic dynamics: the northern migration of a then African island continent to form a land bridge with Eurasia causing a colder Antarctic and significantly hotter tropical climates as they are today (Woodruff et al., 1991). The overall hotter climate in the tropics due to an interrupted oceanic circulation likely played a part in forming an arid region in northeastern Mexico that currently separates the ranges of *C. serpentina* and *C. rossignonii*. In this scenario the arid region time of emergence occurred after the dispersion of *Chelydra* into Central America, isolating the ancestral populations of the two species and effectively closing what was once a migration corridor to Central America into a climatic migration barrier. According to Lomolino et al. (2006), this desert region extends to the Gulf of Mexico and is flanked by the transvolcanic highland

belt, an obstacle that extends west to the Pacific Ocean. An alternative hypothesis can be advocated in which *Chelydra* may have taken refuge in Central America and then recolonized North America (Iverson, personal communication, 2013).

Chelydra rossignonii and *C. acutirostris* are estimated to have diverged from a common ancestor 4.25–8.5 Ma (Phillips et al., 1996). This divergence coincides with the initial formation of the Panamanian Land Bridge (Panamanian Isthmus) approximately 7 or 8 Ma (Simpson, 1980; Flynn et al., 2005) that allowed biotic interchanges between North-Central America and the previously isolated island continent of South America.

Chelydra serpentina

A succession of alternating glacials and interglacials impacted the northern range of *C. serpentina* during the Pleistocene starting 2.5 Ma. The last and largest, the Wisconsinan glacial advanced through the central lowlands of Ohio as far south as the Ohio River at latitude 39°N by 18 ka (Frenzel, 1973; Kurtén, 1988). The decrease in temperature in North America resulted in treeless tundra along the ice-sheet's margin and small isolated regions southward along the Appalachian highlands to northern Georgia (Gates, 1993). The Wisconsinan climate in North America was sufficiently cold to permit the invasion of extant subarctic herds of Muskox, *Ovibos moschatus*, as far south as New York and Ohio (Kitts, 1953; McDonald and Davis, 1989).

The change in the range of *C. serpentina* in response to these glacial advances is not well understood. Proxy estimates for the decrease in temperatures can be obtained by utilizing the paleobotanical record and changes in the ranges of three North American tree genera sensitive to climate 18 ka (data given for eastern North America; Gates, 1993). The present southern range limit of cold-resistant *Picea* (spruce), an aggressive pioneer genus, roughly approximates the northern range boundary of *C. serpentina* which today is located at a northernmost latitude of 51°N. This exclusivity is more evident with the phytogeography of another evergreen, *Abies* (firs). Roughly where this tree genus ranges, *C. serpentina* does not (Eckenwalder, 2009). The ranges of *C. serpentina* and *Abies* are mutually exclusive over the entire North America continent.

In contrast the modern ranges of two other tree genera, *Quercus* (oaks) and *Carya* (hickory), both approximate the range of *C. serpentina*. *Picea* forests today are limited to mid northeastern Canada, but during the Wisconsinan glacial maxima 18 ka they extended along the Mississippi River as far south as the Gulf Coast of Louisiana (Ruddiman and Wright, 1987; Davis and Shaw, 2001). *Picea* forests at such low latitudes suggest that the southern North American climate in the Pleistocene had an ecosystem shift similar to climates currently found in the temperate northern latitudes of Canada, where *C. serpentina* does not range (Gibbons et al., 1988). The presence of *Picea* along the Mississippi River and the accompanying cooler climate is attributed to glacial meltwater from the Laurentide ice sheet draining via the Mississippi River and its delta into the Gulf of Mexico. Unlike today, 18 ka the cold narrow region bisected the range of *C. serpentina* (this is not as obvious in the isotherm map of Figure 3), which promoted

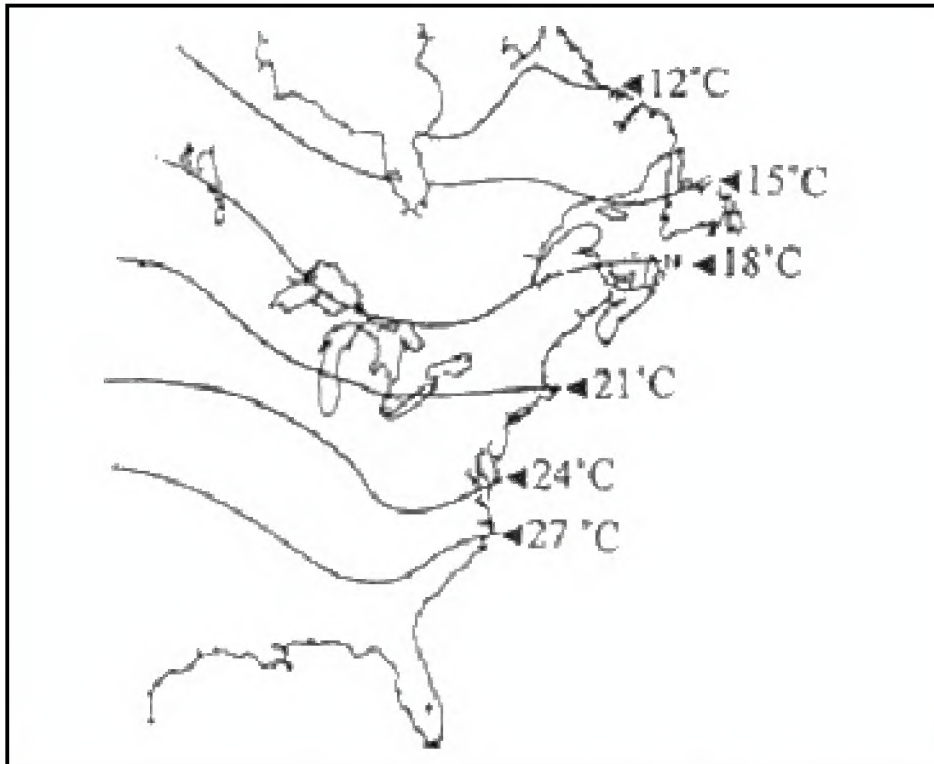


Figure 2. The present-day mean July temperature isotherms of eastern North America (modified from Wright et al., 1993). Note the correlation between the 18°C mean July isotherm and the northern range limit of *Chelydra serpentina* shown in Figure 1. Mean July temperatures of 18°C are apparently the lower limit critical for *C. serpentina* egg incubation (Holman and Andrews, 1994).

genetic distance of the flanking populations through a combination of spatial variation and then isolation. The paleobotanical data suggest that the Mississippi River and nearby regions along its banks throughout its northern course sustained temperatures too low to maintain breeding populations of *C. serpentina* (to be discussed later). A similar geological circumstance occurred on a much longer, grander scale during the Late Cretaceous about 100 Ma when North America was divided into the two island continents of Laramidia and Appalachia. The inland sea that formed these islands was such a significant isolation event that it is thought to have fostered turtle speciation (Lively, 2015).

The absence of *Picea* from southern North America by 12 ka corresponds with the capture of meltwater flow from the Laurentide ice sheet by the Saint Lawrence River (Broecker et al., 1960). The transformation of the now warmer Mississippi River from a migration barrier to a migration corridor united the once isolated populations of *C. serpentina* on either side of the river. The *C. serpentina* polymorphisms that varied from the predominant CR mtDNA haplotype in the Mississippi River Delta (Walker, Moler et al., 1998) correlate with the southern location of this divisive event. Genetic isolation is further promoted by the flow of the Mississippi into the delta with divergent distributaries (delta river branches) making it more likely for CR mtDNA polymorphisms to be isolated. The detailed data reported by Walker and Avise (1998) support this hypothesis where five of the six polymorphisms (identical in sequence) were reported in high concentration in the lower Mississippi delta of Louisiana (the delta is generally known for its high biodiversity). The opposite is true farther north and upstream in southern Missouri where tributaries of the Mississippi River drainage converge and no polymorphisms were observed. This scenario can be expanded to propose a natural archiving mechanism whereby polymorphisms congregate downstream by the southern flow of the Mississippi drainage (a system that occupies roughly a third of the United States). As the tributaries converge, the polymorphisms eventually are retained as viable

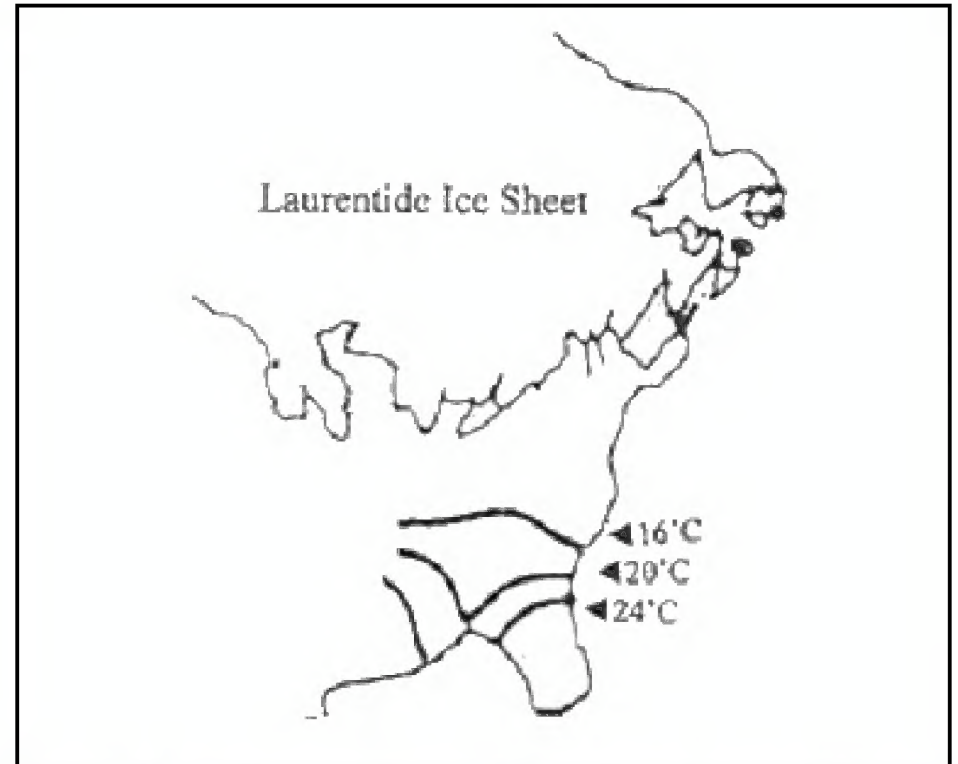


Figure 3. The North American mean July isotherms estimated from pollen analysis 18 ka (modified from Wright et al. [1993] and Holman and Andrews [1994]). Note that the 18°C mean July isotherm (between the 16°C and 20°C isotherms), a correlate of the northern range limit of *Chelydra serpentina*, shifted south from its current position of 51°N latitude in Canada to 35°N in northern Georgia 18 ka. This late Pleistocene climate reduced the current range of *C. serpentina* by roughly 70%.

populations in the catch basin of the delta, constrained by the southern flow of the river drainage and the impenetrable migration barrier of the Gulf of Mexico.

The range reduction of *Quercus* and *Carya* forests and the southward shift of their northern margins 18 ka to latitude 35°N suggest that the northern range of *C. serpentina* shifted from southern Canada to the southern United States in response to global cooling. Adults of *C. serpentina* tolerate seasonal cold temperatures by submersion in waters that are too deep to freeze solid. Hibernation can promote adult *C. serpentina* populations in cool northern climates by migration. But for sustainable reproducing populations, embryonic *C. serpentina* are restricted to development in vulnerable subterranean nests limited to regions with a critical temperature range needed for incubation.

Neonatal *C. serpentina* have limited ability to recover from subzero temperatures and rarely overwinter in their nests (Yntema, 1976). A review of the ranges of all North American turtles indicates that none extend beyond the 18°C mean July isotherm shown in Figure 2 (Behler and King, 1979). A mean July temperature < 18°C provides too low of a ground incubation temperature for the eggs of *C. serpentina* to hatch (Holman and Andrews, 1994). The northern edge of the current range of *C. serpentina* shown in Figure 1 correlates well with the present 18°C mean July temperature isotherm shown in Figure 2. Likewise, *Chrysemys picta* (Painted Turtle), another cold-tolerant species of turtle whose transcontinental range uniquely among chelonians spans the Atlantic to the Pacific coasts also follows this isotherm boundary. The few reptiles that do range north of the 18°C mean July isotherm such as *Thamnophis sirtalis* (Common Garter Snake) are ovoviviparous with females retaining the eggs within their oviducts. The thermoregulatory behavior of the parent provides adequate incubation temperatures for live birth (Steyermark et al., 2008).

Figure 3 displays the inferred mean July isotherms based on paleontological pollen data of tree species 18 ka. The 18°C mean July isotherm (estimated between the 16°C and 20°C mean July temperature isotherms) can also be used to reconstruct northern range boundaries of *C. serpentina* in the past. A comparison with the present 18°C mean July isotherm shown in Figure 2 and an estimate of the 18 ka mean July isotherm in Figure 3 indicate that the northern limit of *C. serpentina* was reduced by a roughly 2000-km shift from present-day Manitoba (51°N latitude) to the southern state of Georgia (35°N latitude) during the Wisconsin glacial maximum. The low genetic diversity of *C. serpentina* can be explained by the species experiencing population bottlenecks (*C. serpentina* on the Florida Peninsula experiences a very different kind of bottleneck to be discussed later). Genetic bottlenecks are characterized by a severe population depression that is indicative of a catastrophic (genetic diversity-reducing) event followed by a characteristic population and range expansion.

The second requirement for a genetic bottleneck, rapid range expansion or recolonization, is addressed by behavioral and paleontological studies. Behavioral studies on *C. serpentina* indicate both males and females migrate, but the migration distance of nesting female *C. serpentina* was measured up to 0.5 km for terrestrial migrations and 8 km for aquatic migrations (Obbard and Brooks, 1981; Sloan and Lovich, 1995). Walker, Moler et al. (1998) remarked that land migrations measured kilometers in length. In contrast, the closely related *M. temminckii* has been observed to move a maximum of 1.8 km in aquatic habitats and is not known for extensive land migrations (Pritchard, 1989; Trauth et al., 1998). Another turtle taxon, *Terrapene carolina triunguis* (Three-toed Box Turtle), has transients within its populations (Schwartz et al., 1984). Transients represent a small percentage of highly mobile mostly young males that characteristically have no home range. Observed to travel abnormally long straight-line distances up to 10 km in 15 months, they provide a mechanism for gene flow between otherwise isolated resident and sedentary *T. c. triunguis* populations, (home ranges of nontransient *T. c. triunguis* average 0.13 km²). An exhaustive literature survey produced no investigations on the existence of transients within populations of *C. serpentina*, although an argument can be made that females of this species with their abnormally long nesting migrations function as transients.

Paleontological studies also provide evidence that *C. serpentina* is an aggressive colonizer. This is supported by its presence and the absence of other turtles, with the exception of *C. picta*, in a kettle bog site in Ohio, shortly following the retreat of the glacier from the region. Radiocarbon dates indicated the turtle remains were 10,000 years old, though the reference did not date the lapse of time between glacial retreat and recolonization by *C. serpentina* (Holman and Andrews, 1994). However an estimate can be made from the data of Wright et al. (1993). The glaciers retreated from Ohio at least 15 ka, but the mean July temperature >18°C required by *C. serpentina* for egg incubation did not occur until between 12 and 9 ka at this latitude. It can be concluded that conditions favorable for recolonization of the Ohio site by breeding populations of *C. serpentina* after the Wisconsin glacial retreat 15 ka lagged behind 6,000 to 3,000

years (between 9 ka and 12 ka) based on the findings of Wright et al. (1993). This estimate is supported by *Chelydra* fossils recovered from the Sheridan Pit, Wyandott County, Ohio within sediments dated between 10,470±70 and 13,120±80 ya (Redmond and Tankersley, 2005). The cave was covered by glacial ice and did not open to the surface until after deglaciation of the area roughly 14 ka.

Further support of strong colonizing ability by *C. serpentina* is provided by other salient paleontological evidence. Unlikely to be isolated accidental excursions from their range, fossil extralimital remains indicate that *C. serpentina* colonized west of the North American continental divide in Nevada (van Devender and Tessman, 1975) where it was found along the Colorado River and Idaho on the Snake River as part of the Sangamonian American Falls Fauna (Pinsof and Akersten, 1988; Pinsof, 1998). In both cases these archaic *C. serpentina* populations represented by the two fossil sites may have exploited Lake Bonneville. The Great Basin, where this lake was once found has a repeated history of large bodies of water (possibly forming as many as 28 times over 3 million years). The last of these lake incarnations, existing from 32 to 14 ka, was about as large as Lake Michigan. It was reduced by a factor of ten in surface area as it transitioned into the Holocene leaving the Great Salt Lake as a remnant (Lake Bonneville was sustained by a natural earthen dam at Red Rock Pass which was breached forming a great flood of the Snake River 14 ka). This pluvial lake may have been a staging ground in a stepwise western range advance that expanded to Las Vegas via the multitude of minor Pleistocene lakes that dotted the intervening region. The then cooler temperatures and higher precipitation in the western Great Basin, possibly caused by a more southerly polar jetstream, also provided favorable conditions for colonization, a climate then seemingly more like the current Great Lakes region where *C. serpentina* ranges. Presently Las Vegas (36°N latitude) has a mean July temperature of 32°C, while that of the American Falls Reservoir (43°N latitude) is 21.4°C. The present-day absence of *C. serpentina* can be explained by the observation that eggs of this species incubated at (constant) high temperatures ≥32.5°C do not develop (ask.com.weather, n.d.; Yntema, 1978). This does not explain its absence from the American Falls Reservoir today, which is well south of its northernmost range limit in Manitoba at 51°N (COSEWIC, 2008). The extirpation of *C. serpentina* from the American Falls Reservoir in Idaho may be attributable to the aridity of the region which also can hamper embryonic development (Lynn and Ullrich, 1950; Bartholomew et al., 1980). Currently the American Falls Reservoir receives 307 mm of precipitation annually and the Las Vegas area 114 mm. Today the southeastern boundary of arid environments in North America generally starts at the 100° meridian. The western range boundary of *C. serpentina* roughly follows the 105° meridian which corresponds closely with the isohyet of 200–400 mm annual precipitation (Bartholomew et al., 1980). Hence, low precipitation (caused by the rain shadow of the Rocky Mountains) as well as high temperature created regional source reductions. This lack of good nesting sites likely played a critical role in recruitment failure (lack of offspring to replace adults) and defined the western border of the current range of *C. serpentina*.

Rapid re-colonization into a large area from glacial forest

refugia results in low genetic variation in populations compared to a slow re-colonization that will produce a higher degree of genetic variation in the newly colonized region (Hewitt, 1999). An explanation for the small pockets of genetic variation with *C. serpentina* can be gained again from Wright et al. (1993). Regions that deviate from the predominant CR mtDNA, the Mississippi Delta, portions of South Carolina, and Arkansas, all had remnant *Carya* and *Quercus* forests 18 ka (though the haplotype from Indiana does not fit this model). These forests suggest the presence of glacial refugia at this time which may have preserved small subpopulations with pre-Pleistocene *C. serpentina* CR mtDNA haplotypes. During the glacial retreats, the turtle recolonized previously lost territory up to southern Canada while retaining the predominant CR mtDNA haplotype and maintaining smaller southern refugia populations consisting of minor haplotypes. The glacial range reductions and the ability to migrate relatively large distances may have combined to provide favorable conditions for low genetic diversity in recolonized territory, subsequently producing a lack of genetic variation. This lack of genetic variation is further supported by a study on *Kinosternon flavescens* (Yellow Mud Turtle) that has a southwestern distribution in North America, but has less polymorphic CR mtDNA in the northern portion of its range (Serb et al., 2001).

The present range of *C. serpentina* in Florida is vulnerable to another type of genetic bottleneck caused by marine flooding of the coast by sea level rise during interglacials (Alt and Brooks, 1965). The decay of the ice sheets during interglacials increased ocean volume, which covered the low-lying land areas of the Florida Peninsula (Figure 4). Marine environments are lethal to this stenohaline species of freshwater turtle (Kinneary, 1993). To what degree the flooding of the Florida Peninsula during interglacials reduced the range of the *C. serpentina* peninsular population is not completely understood. The interglacial Florida Archipelago which formed from the flooding was unlike



Figure 4. A reconstruction of the southeastern United States and Central American shorelines during the glacial and interglacial periods of the late Pleistocene Epoch modified from Biknevicius et al. (1993). Shaded areas represent the land area exposed 20 ka by the 118-m lowering of sea level during the Wisconsin glacial period. The inner border corresponds to the projected shoreline caused by the sea-level rise during the mid-Sangamonian interglacial 125 ka. Note the nearly complete interglacial submergence of the Florida Peninsula and comparatively low marine flooding of Veracruz along the northern base of the Yucatan Peninsula, the site of several refugia and the northern range limit of *Chelydra rossignoni*.

the relatively stable oceanic island isolations found on the volcanic Galapagos Island arc that formed 3 Ma with some estimates of up to 9 Ma (Anonymous, 1992). The inherent high altitude volcanic regions of Isabela Island would also provide refugia for its tortoises (*Chelonoidis* spp.) during interglacial marine transgressions. Interestingly the depth of the Pacific Ocean between over half of the major islands within the Galapagos chain is 200 m (Instituto Geográfico Militar del Ecuador, 1981) which is the same depth of the Caribbean Ocean on the western side of Florida that glaciation exposed due to sea level reduction, doubling the land area of the peninsula (Bartholomew et al., 1980). It would suggest an alternate method of migration between those Galapagos Islands emerging from this 200-m submarine plateau during glacial periods. These islands would have merged to form one large island promoting land migration of animal population between what are now islands rather than marine waif dispersion (Instituto Geográfico Militar del Ecuador, 1981). The low-lying sedimentary continental islands that comprised the interglacial Florida Archipelago had a majority of geological features all under 100 m in altitude along what was once the ancestral southern peninsula (Alt and Brooks, 1965). This would restrict the peninsular populations, both terrestrial and freshwater aquatic, to islands vulnerable to complete submersion by catastrophic interglacial marine transgressions.

According to Zug (1968), one extreme transgression occurred during the Aftonian interglacial 1.1 Ma when the Florida Peninsula transitioned into an insular continental archipelago which by continued marine flooding became completely submerged with the exception of one small island near the southern drainage basin. Peninsular populations of *C. serpentina* survived in Florida during this interglacial as an ancestral refuge population in the Florida Panhandle mainland or the base of the peninsula until oceanic levels receded during the Kansan glacial 600 ka. Expanding island landmasses on the Florida Archipelago and a growing land bridge south along the Ocala uplift, a ridge that runs south along the length of Florida (Brooks, 1965), provided a migration corridor for peninsular populations to have recolonized the newly re-forming Florida Peninsula. The subsequent Yarmouthian (600 ka) and Sangamonian (250 ka) versions of the Florida Archipelago had more numerous and larger islands during the interglacial flooding that likely were inhabited by *C. serpentina*. Both interglacials allowed an expansive episode where peninsular populations established themselves on the growing peninsula during the subsequent glacials, staving off range expansion from the north by continental *C. serpentina*. This period effectively ended island isolation yet provided enough isolation for peninsular populations to develop and retain their own morphological characteristics but not sufficient time to accumulate distinct mitochondrial haplotypes which as a rule take at least one million years for one percent mutation, possibly longer with turtles (Avice et al., 1992). The periodic rather than constant reproductive isolation combined with the short time-span is just one cause for the lack of subspeciation. The asymmetric contact of the greatly reduced Aftonian interglacial range of Florida *C. serpentina* with the continental range of *C. serpentina* may explain why the former did not undergo complete speciation, or subspeciation.

In summary, the range loss of peninsular *C. serpentina* during the interglacials was followed by more than a doubling of the Peninsula's current land area during the Wisconsin glacial period (Kurtén, 1988; Biknevicus et al., 1993). The Florida Peninsula then was mostly successional sand dunes and prairie (Gates, 1993), but presumably had aquatic habitats suitable for peninsular populations of *C. serpentina*. The episodic range reductions and expansions of peninsular populations of *C. serpentina* during the interglacial and glacial periods occurred alternately to the range reductions and expansions of continental populations of *C. serpentina*. While the range of continental *C. serpentina* contracted toward the south during the Wisconsin glacial period, the range of peninsular populations of *C. serpentina* was expanding due to lowering of the sealevel. Conversely, during the last interglacial period, the range of *C. serpentina* on the Florida Peninsula contracted by marine flooding while the range of continental *C. serpentina* underwent an expansion by recolonization of land exposed by the retreat of the glaciers. This dynamism created by such an unstable geological and climatic history in North America provided many occasions favorable for *C. serpentina* population bottlenecks in both regions under opposing circumstances.

One major unanswered question remains (Walker, Moler et al., 1998): why do the two populations (continental and peninsular) share the same predominant CR mtDNA haplotype? Similar circumstances existed in the Pleistocene during which each population alternately underwent a range reduction during glacials and interglacials allowing them to be genetically swamped by the explosively expanding population. The current range of peninsular populations of *C. serpentina* was severely reduced during the Sangamonian interglacial, expanded its range on the growing Florida Peninsula during the Wisconsin glacial period followed by the migration of continental populations of *C. serpentina*. In this scenario the two turtle populations interbred to form an intergrade sharing the same mtDNA.

Temperature-dependant sex determination (TSD) observed in *C. serpentina* may lend support to asymmetric breeding proposed by a Gyllensten and Wilson hypothesis (1987) as an adaptive mechanism for range expansion during the fluctuating glacial-interglacial climates of North America. Gender selection of *C. serpentina* eggs incubated at constant temperatures either above 30°C or below 21°C favored the hatching of 100% females (eggs incubated constantly above 32.5°C or below 18°C do not develop) while intervening temperatures within this range developed mainly males (Yntema, 1976, 1978). TSD can be interpreted as providing an increased reproductive rate (more females) at the temperature extremes of the northern and southern range boundaries of *C. serpentina*, which might compensate for hatchling mortality due to these thermal extremes.

The present area of contact between the ranges of continental and peninsular *C. serpentina* at the base of the Florida Peninsula has a mean July temperature of 28°C (ask.com.weather, n.d.). Likely this value was higher during the warmer interglacial periods resulting in higher ground temperatures and hatching proportionally greater numbers of *C. serpentina* females because of TSD. The climate of northern Florida would then promote local resident populations consisting of an abnormally high number of

female continental *C. serpentina* poised to migrate into the Florida Peninsula (the opposite may occur during glaciations). The *veni, vidi, vici* aspect of this climatically spurred southern migration is enhanced by the geographical funneling effect of a much greater continental *C. serpentina* population inhabiting the larger southeastern North American landmass to the much smaller Florida Peninsula. Asymmetric interbreeding by the inherent larger number of migrating continental females and lower number of resident peninsular males would occur when the archipelago was converted back to a peninsula during glacial period. Support for this mechanism is observed in similar reproductive compensation with female *Aldabrachelys gigantea* (Aldabran Tortoise). This species has greater fecundity (based on number of eggs observed in the ovaries) in the coastal region of the Aldabra Atoll compared to females found inland (Swingland and Lessells, 1979). Through intraspecific differential reproduction, increased egg output offsets the high mortality in coastal areas where the availability of shade from the intense tropical sun is less abundant. In both cases, *A. gigantea* and *C. serpentina*, through different reproductive mechanisms, the former by a direct increase in egg production while the latter favoring a greater number of egg-producing continental females, have an increased reproductive proclivity. *C. serpentina* under this mechanism in northern and southern climatic extremes (northern and southern range limits) would have higher embryonic mortality which would be countered by a higher number of egg-producing females. Phenologic modeling on *Chrysemys picta* (Painted Turtle) supports this prediction of climatic influences causing skewed sex ratios (Telemeco et al., 2013).

A literature survey provided no information on the sex ratio of *C. serpentina* in its southern range such as northern Florida. However, a study by Punzo (1975) on peninsular populations trapped 34 male and 25 female from a 50-acre woodland and swamp tract in Sarasota County. Although the objective of this study was not to determine the sex ratio, it does suggest incidentally that TSD in this region currently favors male *C. serpentina* where the mean July temperature is 28°C (ask.com.weather, n.d.). Although the present-day current sex ratio would favor the Gyllensten and Wilson (1987) hypothesis (a proportionately greater number of male peninsular *C. serpentina* and invasive female continental *C. serpentina* interbreeding), the warmer interglacial period likely favored female peninsular *C. serpentina* if this population has the same TSD sex ratios at various incubation temperatures as continental *C. serpentina* populations. There are other problems with applying the Gyllensten and Wilson hypothesis of asymmetric mtDNA gene flow. A relict population has yet to be found of peninsular *C. serpentina* with CR mtDNA different than the predominant CR mtDNA of *C. serpentina*. This absence is problematic to this hypothesis. Another need is the genetic analysis of peninsular *C. serpentina* nuclear DNA to test if it too is closely related to the continental genome or polymorphic to it. However, the Phillips et al. (1996) study did suggest that in some individuals there are other mtDNA domains of peninsular *C. serpentina* that are polymorphic to the mtDNA domains of continental *C. serpentina*.

Absence of *Chelydra rossignoni* in regions of Central America

The CR mtDNA of peninsular *C. serpentina* is identical to

the predominant CR mtDNA haplotype of continental *C. serpentina* (Walker, Moler et al., 1998), suggesting that these two populations are genetically equally distant from *C. rossignonii*. In contrast, the morphology of Florida population most closely resembles *C. rossignonii* (Pritchard, 1979). One characteristic that both populations share is pointed protuberances (fleshy spikes around the neck: Pritchard, 1979) which are thought to increase skin surface area for cutaneous respiration in the inherently oxygen-poor warm water of tropical regions (continental *C. serpentina* have rounded protuberances; it is still a matter of argument whether this morphology is genetic or developmental due to tropical temperatures). *Chelydra serpentina* and *C. rossignonii* are presently separated by approximately 800 km along the coast of the Gulf of Mexico between northern Mexico and southern Texas (Figure 1). When this range gap developed is a matter of conjecture. Possibly before the climatic changes of Miocene, *Chelydra* had a continuous range, presently interrupted, from southern Texas through Central America. This is supported by Phillips et al. (1996) who dated the isolation of *C. rossignonii* from *C. serpentina* at between 11.12 to 22.25 Ma. It is likely that fossil material of this species is yet to be found in northeastern Mexico, just as the fossils of extirpated *C. serpentina* have been found in southern Nevada (van Devender and Tessman, 1975) and the American Falls Reservoir (Pinsof and Akersten, 1988; Pinsof, 1998).

The hiatus between the ranges of *C. rossignonii* and *C. serpentina* in northeastern Mexico coincides with a climatic hot spot roughly centered in this region. This area has experienced a temperature of 58°C (136.4°F), and has mean annual precipitation of 406–610 mm (Bartholomew et al., 1980). Although this is not the official recorded high of 56.6°C (134°F on 10 July 1913) of Death Valley, California (NOAA National Climatic Data Center, n.d.), the region could be interpreted as an intense climatic land migration barrier which impeded contact between the ranges of *C. serpentina* and *C. rossignonii*. High temperatures combined with inherently decreased soil humidity provide poor soil conditions for embryonic development. Arid soils increase egg desiccation, increasing both egg mortality and embryonic deformities suggesting low fitness anatomical anomalies (Lynn and Ullrich, 1950).

A similar arid dry forest is found in the Yucatan Peninsula where *C. rossignonii* also does not range. The absence of *C. rossignonii* can be attributed to the peninsula's porous limestone geology that sustains widely dispersed rivers and few lakes or other bodies of surface water (Lee, 1980) making overland dispersal from one aquatic habitat to another by a species vulnerable to dehydration unlikely. In contrast, though Florida has roughly the same mean annual precipitation as the lower Yucatan Peninsula (Bartholomew et al., 1980) and is also a peninsula primarily composed of limestone (Alt and Brooks, 1965), the relatively lower land elevation and high water-table promotes an abundance of surface rivers (Telford, 1965), migration corridors useful for recolonization by *C. serpentina* of the Florida Peninsula. Stuart (1966) attributed a subterranean drainage system of the Yucatan Peninsula (higher elevation and deeper aquifer) for the relatively low number of surface streams on the Yucatan Peninsula. Rivers are numerous in the more mountainous southern Belize where *C. rossignonii* occurs (Moll

and Dodd, 1985).

Ranges of *Chelydra rossignonii* and *Chelydra acutirostris*

Control region mtDNA from three *Chelydra rossignonii* specimens, two from Mexico and one from Honduras, were each slightly different (Steyermark et al., 2008). The environmental history of *C. rossignonii* may have differed from that of the North American species by not experiencing climatic changes that severely reduced their current ranges. The range of the Central American species shown in Figure 5 was geographically isolated from the causes of genetic bottlenecks experienced by the North American population. While marine transgressions flooded the range of *C. rossignonii* during the last interglacial, such flooding was minor in comparison with interglacial marine flooding of Florida (compare Figures 4 and 5A). Evidence for this stable environment is provided by the presence of Pleistocene refuges embedded within the range of *C. rossignonii*. The Pleistocene Refuge Hypothesis (PRH; Whitmore and Prance, 1987) proposes that the modern environment is stable, and that the vegetation and climate are unchanged from the Pleistocene. Figures 5a and 5b show that a significant portion of the northern range of *C. rossignonii* incorporates six refugia that have remained unchanged for 10 ka (Prance, 1982; Whitmore and Prance, 1987). Genetic diversification may have been enhanced by the inherent insularity of the seven refugia creating favorable conditions for the development of metapopulations each with different predominant CR mtDNA haplotypes. Though we do not know it to be a fact, the seven proposed *C. rossignonii* refugia populations each acting as clustered centers of diversity were in close enough proximity that they likely merged to form the present continuous range of *C. rossignonii* with a population possessing polymorphic CR mtDNA.

Figures 6A and 6B illustrate the refugia found within the southern range of *C. acutirostris*. Both the range and refugia have little variation from one another as they terminate at the Gulf of Guayaquil (Whitmore and Prance, 1987; Gibbons et al., 1988). Interestingly there are no refugia in the northern range of *C. acutirostris* (southern Honduras and Panama) which suggests the region acted as a migration barrier during the Pleistocene glaciations. The nearest distance between Pleistocene refugia within the range of *C. rossignonii* and the Pleistocene refuge within the range of *C. acutirostris* roughly match the current gap

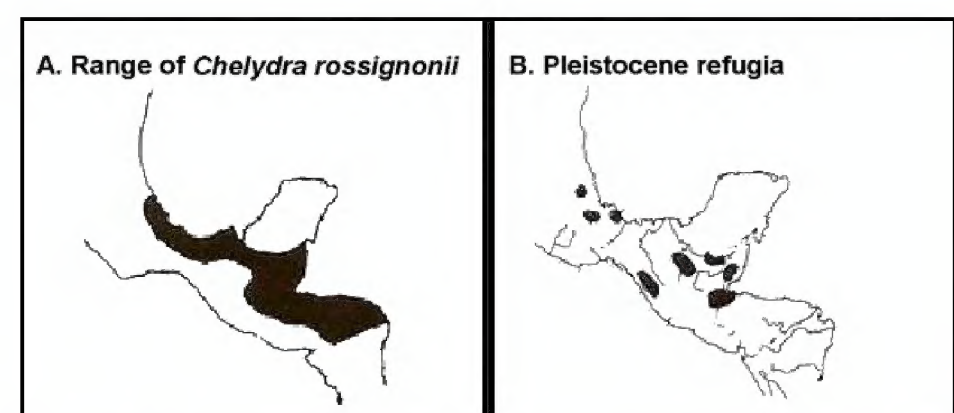


Figure 5. The range of *C. rossignonii* in Central America (modified from Gibbons et al., 1988) compared to a map of Pleistocene refugia for the same region (modified from Whitmore and Prance, 1987). The two maps indicate an overlap of seven discrete climatically stable refugia. These refugia may have prevented genetic bottlenecks and preserved or promoted CR mtDNA polymorphisms. Note that some refugia are connected by a branched river system which can promote gene flow and lower CR mtDNA polymorphisms.

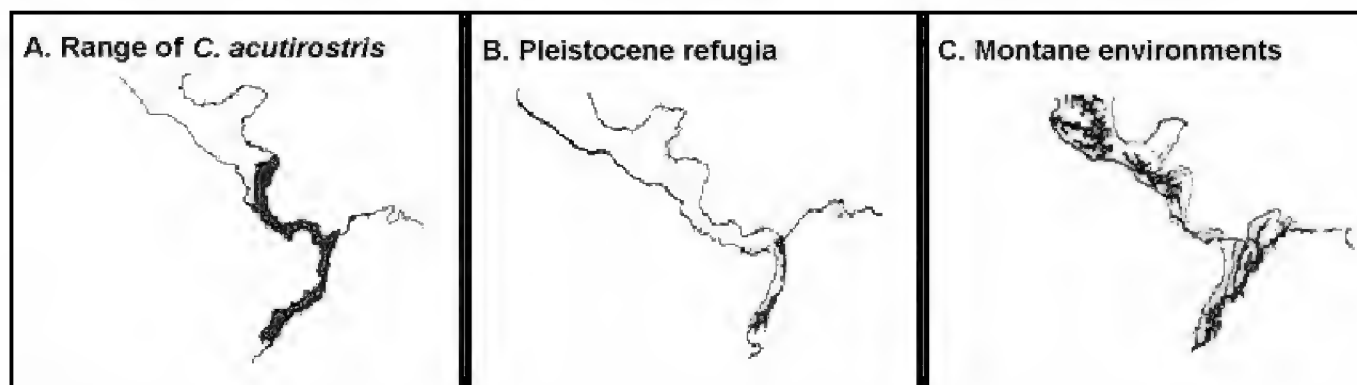


Figure 6. The range of *C. acutirostris* in Central and South America (modified from Gibbons et al., 1988) compared to overlapping Pleistocene refugia and montane environments of the same region (modified from Whitmore and Prance, 1987, and Bartholomew et al., 1980). The range of *C. acutirostris* incorporates one continuous climatically stable Pleistocene refugium. Arid and montane environments of the Andes restrict the range of *C. acutirostris* to the northern Pacific Coast of South America, preventing colonization farther south into Peru. The rivers in this area run parallel off the Andes to the Pacific Ocean, and are thought to promote CR mtDNA polymorphisms through their inherent isolation.

distance between the ranges of *C. rossignonii* and *C. serpentina* in northern Mexico. The refugia suggest that ancestral population of the Central and South American species may have experienced an isolating periodic disjunction during multiple glaciations and then re-expanded their ranges during the interglacial periods. This allopatric speciation is supported by an observation made on the range of another Central American species *Kinosternon leucostomum* (White-lipped Mud Turtle). The ranges of the two subspecies of this turtle (*K. l. leucostomum* and *K. l. postinguinale*) roughly occupy the same combined range of *C. rossignonii* and *C. acutirostris*. The *K. l. leucostomum* / *K. l. postinguinale* range boundary is roughly 400 km south of the *C. rossignonii* / *C. acutirostris* range boundary (Berry and Iverson, 2001). This may suggest that in Honduras a migration barrier exists or existed during predicted range reduction of the last interglacial. These range reductions may not have been as severe as in North America, causing possible genetic bottlenecks, but they did provide enough isolation between subpopulations to promote speciation. This is unlike the contact between the ranges of mainland and peninsular *C. serpentina* populations in northern Florida where the interglacial peninsular land mass became smaller and no speciation or subspeciation occurred.

Several observations can be made from Figures 5B and 6B that influence range size and genetic diversity. Noteworthy is that late Pleistocene refugia found within the current range of *C. acutirostris* are not fragmented compared to the refugia found in the range of *C. rossignonii*. This would predict a lower number of isolated metapopulations and lower genetic diversity in the latter. Contrary to this prediction, limited genetic sequence data of the CR mtDNA of two *C. acutirostris* from Panama and Ecuador indicated that they had the greatest intraspecific genetic divergence of *Chelydra* in the study (estimated from phylogram branch lengths, Steyermark et al., 2008). One possible explanation is that rivers found in the range of *C. rossignonii* are more dendritic: branching through each refugia decreasing the isolation between populations. The opposite is true for the refugia found in the range of *C. acutirostris*: the rivers are mainly parallel in nature as they flow through coastal deserts to the Pacific from their source in the Andes, in effect, restricting *C. acutirostris* to a series of episodically dedicated riparian populations. The PRH applied to the range of *C. acutirostris* as with *C. rossignonii* provides a similar argument for the species escaping

a genetic bottleneck and having polymorphic CR mtDNA. The finding of Phillips et al. (1996) that two specimens of *C. acutirostris*, both from Esmeraldas, Ecuador, had slightly divergent mtDNA that was polymorphic support this hypothesis.

Mean July temperatures $\leq 18^{\circ}\text{C}$, montane, arid, and marine environments are four barriers that restrict the distribution of *C. serpentina* in North America. The South American, Caribbean, and Pacific range boundaries of *C. acutirostris* coincide with three of these geographic barriers. As shown in Figure 6, the southern range limit of *C. acutirostris* at 2°S latitude in southern Ecuador is against a spur of the Andes Mountains, Cerros el Alto Amotape ó de le Brea, which extends to the Pacific coast and is also adjacent to an arid region with a third the annual rainfall (Bartholomew et al., 1980; Prance, 1973). Based on Medem (1977), *C. acutirostris* nests in February, in contrast to May or June for *C. serpentina* (Galbraith, 2008). A reasonable assumption can be made that there is a critical mean monthly temperature (likely in February) of $>18^{\circ}\text{C}$ as with *C. serpentina* that is needed in egg incubation for *C. acutirostris*. At present a mean July temperature of 18°C is found approximately 700 km south beyond the Gulf of Guayaquil near Paramonga, Peru (Latitude 10°S), while the mean January temperature in the austral summer (closer to the nesting time observed with *C. acutirostris* in February) becomes 18°C even farther south in Chile (ask.com.weather, n.d.). The climatic data suggest that *C. acutirostris* could become established as a breeding population more to the south than the present-day limit, but might be restricted by the amount of annual precipitation. Since *C. acutirostris* clearly does not range beyond the Gulf of Guayaquil, it can be concluded that the Andean Ridge (Figure 6C) and arid dry forests characteristic of Peruvian southern coast, rather than the mean January temperature of $>18^{\circ}\text{C}$, define the southern range limit of *C. acutirostris*. Unlike the northern range limit of *C. serpentina*, this boundary is similar in nature to the extensive western range limit of *C. serpentina* in North America. This narrow hyper-arid coastal desert of South America with its likely laterized soils is as much an impenetrable migration barrier to *C. acutirostris* for colonization as the Pacific Ocean and Andes Mountains. Unlike dendritic river systems, the parallel river systems that originate in the highlands of the Andes are inherently more insular as they drain in a linear fashion into Pacific (this may be a similar reason, though here more extreme, as why *M. temminckii* did not colonize the Atlantic coast of North

America). As with *C. rossignoni* and the few isolated river systems of the Yucatan Peninsula, the rivers of the southern coast of Peru and Chile are apparently too widely spaced in the arid desert to provide a corridor for colonization, impeding a southward range extension into vacant habitat.

Similar geographic restrictions are observed at the easternmost South American range boundary of *C. acutirostris* on the Colombian coast (see Figure 6). An arid forest is bordered in the south by the Cordillera Occidental, a northeastern spur of the Andes. Successive migration barriers are formed by the Lago de Maracaibo that is flanked by two more spurs of the Andes, Sierra de Perijá and Cordillera de Mérida, which themselves extend to the Caribbean Coast (Bartholomew et al., 1980). This trident spur is surrounded by arid dry forests that enhance this region as a migration barrier, further restricting the eastern range expansion of *C. acutirostris*. This is similar to what is observed on the southern Pacific Coast range boundary. Although several other genera such as *Kinosternon* (mud turtles) and *Trachemys* (basking turtles) have crossed this barrier, these genera are more resistant to dehydration (Wygoda, 1990, Goin and Goin, 1971). The small cruciform plastron combined with porous skin of the aquatic *Chelydra* form less protection against dehydration (Goin and Goin, 1971). With these *C. acutirostris* deficiencies, the region provides a more intense migration barrier. The coloniza-

tion of the Amazonian drainage is prevented: a potentially catastrophic event for many potential prey species inhabiting the basin and an expansive bonanza event for *C. acutirostris*.

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Literature Cited

- Alt, D., and H. K. Brooks. 1965. Age of the Florida marine terraces. *Journal of Geology* 73(2):406-411.
- Anonymous. 1992. Data from sea floor could resolve a long-standing controversy. *Iguana Times* 1(4):12.
- Ask.com.weather. n.d. [retrieved May 15, 2008, <http://uk.ask.com/weather/c>].
- Auffenberg, W. 1957. The status of the turtle *Macrolemys floridana* Hay. *Herpetologica* 13(2):123-126.
- Avise, J. C., B. W. Bowen, T. Lamb, A. B. Meylan and E. Bermingham. 1992. Mitochondrial DNA evolution at a turtle's pace: Evidence for low genetic variability and reduced microevolutionary rate in the Testudines. *Molecular Biology and Evolution* 9(3):457-473.
- Bartholomew, J. C., et al. (editors). 1980. *The Times atlas of the world, comprehensive edition*. New York: Times Books. [Plates 4 and 5].
- Behler, J. L., and F. W. King. 1979. *The Audubon field guide to North American reptiles and amphibians*. New York: Alfred A. Knopf.
- Berry, J. F., and J. B. Iverson. 2001. *Kinosternon leucostomum*. *Catalogue of American Amphibians and Reptiles* (724):1-8.
- Biknevicius, A. R., D. A. McFarlane and R. D. MacPhee. 1993. Body size in *Amblyrhiza inundata* (Rodentia: Caviomorpha), an extinct megafaunal rodent from the Anguilla Bank, West Indies: Estimates and implications. *American Museum Novitates* (3079):1-25.
- Bowen, G. J., and J. C. Zachos. 2010. Rapid carbon sequestration at the termination of the Paleocene-Eocene thermal maximum. *Nature Geoscience* (3):866-869. doi:10.1038/ngeo1014.
- Broecker, W. S., W. M. Ewing and B. C. Heezen. 1960. Evidence for an abrupt change in climate close to 11,000 years ago. *American Journal of Science* 258(6):429-448. doi:10.2475/ajs.258.6.429
- Carr, A. 1952. *Handbook of turtles*. Ithaca, New York: Cornell University Press.
- Cope, E. D. 1868. An examination of the Reptilia and Batrachia obtained by the Orton Expedition to Ecuador and Upper Amazon, with notes on other species. *Proceedings of the Academy of Natural Sciences of Philadelphia* 20:96-140.
- COSEWIC. 2008. COSEWIC assessment and status report on the Snapping Turtle, *Chelydra serpentina*, in Canada. Ottawa, Canada: Committee on the Status of Endangered Wildlife in Canada.
- Davis M. B., and R. S. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292:673-679.
- de Blij, H. 2005. *Why geography matters*. New York: Oxford University Press.
- Eckenwalder, J. E. 2009. *Conifers of the world*. Portland, Oregon: Timber Press.

- Ernst, C. H., and R. W. Barbour. 1989. Turtles of the world. Washington, D.C.: Smithsonian Institution Press.
- Feuer, R. C. 1966. Variation in snapping turtles, *Chelydra serpentina* Linnaeus: A study in quantitative systematics. Ph.D. Thesis. University of Utah, Salt Lake City.
- Flynn, J. J., B. J. Kowallis, C. Nuñez, O. Carranza-Castañeda, W. E. Miller, C. C. Swisher III and E. Lindsay. 2005. Geochronology of Hemphillian-Blancan aged strata, Guanajuato, Mexico, and implications for timing of the great American biotic interchange. *Journal of Geology* 113(3):287-307.
- Frenzel, B. 1973. Climatic fluctuations of the Ice Age. [translation by A. E. M. Nairn of *Die Klimaschwankungen des Eiszeitalters*]. Cleveland: The Press of Case Western Reserve University.
- Galbraith, D. A. 2008. Population biology and population genetics. Pp. 168-180. *In*: A. C. Steyermark, M. S. Finkler and R. J. Brooks, editors, *Biology of the snapping turtle (Chelydra serpentina)*. Baltimore: The John Hopkins University Press.
- Gates, D. M. 1993. Climate change and its biological consequences. Sunderland, Massachusetts: Sinauer Associates.
- Gibbons, J. W., S. S. Novak and C. H. Ernst. 1988. *Chelydra serpentina*. *Catalogue of American Amphibians and Reptiles* (420):1-4.
- Goin, C. J., and O. B. Goin. 1971. Introduction to herpetology. San Francisco: W. H. Freeman and Company.
- Gyllensten, U., and A. C. Wilson. 1987. Interspecific mitochondrial DNA transfer and the colonization of Scandinavia by mice. *Genetic Research* 49(1):25-29.
- Halliburton, R. 2004. Introduction to population genetics. Upper Saddle River, New Jersey: Pearson Education.
- Hewitt, G. M. 1999. Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* 68:87-112.
- Holman, J. A., and K. D. Andrews. 1994. North American Quaternary cold-tolerant turtles: Distributional adaptations and constraints. *Boreas* 23(1):44-51.
- Holman, J. A., and R. M. Sullivan. 1981. A small herpetofauna from the type section of the Valentine Formation (Miocene, Barstovian), Cherry County, Nebraska. *Journal of Paleontology*, 55(1):138-144.
- Hutchison, J. H. 2008. History of fossil Chelydridae. Pp. 14-30. *In*: A. C. Steyermark, M. S. Finkler and R. J. Brooks, editors, *Biology of the snapping turtle (Chelydra serpentina)*. The John Hopkins University Press, Baltimore.
- Instituto Geográfico Militar Del Ecuador. 1981. República Del Ecuador, Provincia de Galapagos (map insert). Ministro de Relaciones Exteriores.
- Kinneary, J. J. 1993. Salinity relations of *Chelydra serpentina* in a Long Island estuary. *Journal of Herpetology* 27(4):441-446.
- Kitts, D. B. 1953. A Pleistocene musk-ox from New York and the distribution of the musk-oxen. *American Museum Novitates* (1607):1-8.
- Kunzig, R. 2011. World without ice. *National Geographic* 220(4):90-109.
- Kurtén, B. 1988. Before the Indians. New York: Columbia University Press.
- Lee, J. C. 1980. An ecogeographic analysis of the herpetofauna of the Yucatan Peninsula. University of Kansas Museum of Natural History, Miscellaneous Publication 67:1-75.
- Lively, J. R. 2015. A new species of baemid turtle from Kaiparowits Formation (Upper Cretaceous, Campanian) of southern Utah. *Journal of Vertebrate Paleontology* 35(6). DOI: 10.1080/02724634.2015.1009084
- Lomolino, M. V., B. R. Riddle and J. H. Brown. 2006. Biogeography, 3rd edition. Sunderland, Massachusetts: Sinauer Associates.
- Lovich, J. E. 1993. *Macroclmys*, *M. temminckii*. *Catalogue of American Amphibians and Reptiles* (562):1-4.
- Lynn, W. G., and C. M. Ullrich. 1950. Experimental production of shell abnormalities in turtles. *Copeia* 1950(4):253-262.
- McDonald, H. G., and R. A. Davis. 1989. Fossil muskoxen of Ohio. *Canadian Journal of Zoology* 67(5):1159-1166.
- Medem, F. 1977. Contribución al conocimiento sobre la taxonomía, distribución geográfica y ecología de la tortuga “Bache” (*Chelydra serpentina acutirostris*). *Caldasia* 12:41-101.
- Moll, D., and F. J. Dodd, Jr. 1985. New records for *Chelydra serpentina rossignoni* in Belize. *Bulletin of the Maryland Herpetological Society* 21(1):34-37.
- Nekola, J. C., and P. S. White. 1999. The distance decay similarity in biogeography and ecology. *Journal of Biogeography* 26(4):867-878.
- NOAA National Climate Data Center. n.d. [retrieved August 23, 2013, www.ncdc.noaa.gov]

- Obbard, M. E., and R. J. Brooks. 1981. Fate of overwintered clutches of the common snapping turtle (*Chelydra serpentina*) in Algonquin Park, Ontario. *The Canadian Field-Naturalist* 95(3):350-352.
- O'Brian, S. J., D. E. Wildt, M. Bush, T. M. Caro, C. FitzGibbon, I. Aggundey and R. E. Leakey. 1987. East African cheetahs: Evidence for two population bottlenecks? *Proceedings of the National Academy of Sciences* 84(2):508-511.
- Phillips, C. A., W. W. Dimmick and J. L. Carr. 1996. Conservation genetics of the common snapping turtle (*Chelydra serpentina*). *Biological Conservation* 10(2):397-405.
- Pinsof, J. D. 1998. The American Falls local fauna: Late Pleistocene (Sangamonian) vertebrates from southeastern Idaho. *Idaho Museum of Natural History Occasional Paper* 36:121-145.
- Pinsof, J. D. and W. A. Akersten. 1988. Late Pleistocene turtles from the American Falls Reservoir, southeastern Idaho. Abstracts with Programs, 41st Annual Meeting, Rocky Mountain Section. *Geological Society of America* 20(6):463.
- Prance, G. T. 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae, and Lecythydaceae. *Acta Amazonica* 3:5-26.
- . 1982. *Biological diversification in the tropics*. New York: Columbia University Press.
- Pritchard, P. C. H. 1979. *Encyclopedia of turtles*. Neptune, New Jersey: TFH Publications.
- . 1989. *The alligator snapping turtle: Biology and conservation*. Milwaukee: Milwaukee Public Museum.
- Punzo, F. 1975. Studies on the feeding behavior, diet nesting habits and temperature relationships of *Chelydra serpentina osceola*. *Journal of Herpetology* 9(2):207-210.
- Rapoport, E. H. 1982. *Areography: Geographical strategies of species*. New York: Pergamon Press.
- Redmond, B. G., and K. B. Tankersley. 2005. Evidence of early Paleoindian bone modification and use at the Sheridan Cave site (33WY252), Wyandot County, Ohio. *American Antiquity* 70(3):503-526.
- Roman, J. 1997. Cryptic evolution and population structure in the alligator snapping turtle (*Macrolemys temminckii*). Masters Thesis, University of Florida, Gainesville.
- Ruddiman, W. F., and H. E. Wright. 1987. *North America and adjacent oceans during the last deglaciation*. Boulder, Colorado: The Geological Society of America.
- Serb, J. M., C. A. Phillips and J. B. Iverson. 2001. Molecular phylogeny and biogeography of *Kinosternon flavescens* based on complete mitochondrial control region sequences. *Molecular Phylogenetics and Evolution* 18(1):149-162.
- Schwartz, E. R., C. W. Schwartz and A. R. Kiester. 1984. The three-toed box turtle in central Missouri, Part II: A nineteen-year study of home range, movements and population. Jefferson City: Missouri Department of Conservation, Terrestrial Series no. 12.
- Shaffer, H. B., D. E. Starkey and M. K. Fujita. 2008. Molecular insights into the systematics of the snapping turtles (Chelydridae). Pp. 44-49. *In*: A. C. Steyermark, M. S. Finkler and R. J. Brooks, editors, *Biology of the snapping turtle (Chelydra serpentina)*. Baltimore: The John Hopkins University Press.
- Simpson, G. G. 1980. *Splendid isolation: The curious history of South American mammals*. New Haven, Connecticut: Yale University Press.
- Sloan, K., and J. E. Lovich. 1995. Exploitation of the alligator snapping turtle, *Macrolemys temminckii*, in Louisiana: A case study. *Chelonian Conservation and Biology* 1(3):221-222.
- Steyermark, A. C., M. S. Finkler and R. J. Brooks (editors). 2008. *Biology of the snapping turtle (Chelydra serpentina)*. Baltimore: The John Hopkins University Press.
- Stuart, L. C. 1966. The environment of the Central American cold-blooded vertebrate fauna. *Copeia* 1966(4):684-699.
- Swingland, I. R., and C. M. Lessells. 1979. The natural regulation of giant tortoise populations on Aldabra Atoll. Movement polymorphism, reproductive success and mortality. *Journal of Animal Ecology* 48(2):639-654.
- Telemeco R. S., K. Abbott and F. J. Janzen. 2013. Modeling the effects of climate change-induced shifts in the reproductive phenology on temperature-dependant traits. *The American Naturalist* 181(5):637-648.
- Telford, S. R., Jr. 1965. Some biogeographical aspects of Floridian herpetofauna. *Acta Herpetologica Japonica* 2(2):16-21.
- Thomas, T. M., M. C. Granatosky, J. R. Bourque, K. L. Krysko, P. E. Moler, T. Gamble, E. Suarez, E. Leone and J. Roman. 2014. Taxonomic assessment of Alligator Snapping Turtles (Chelydridae; *Macrolemys*), with the description of two new species from the southeastern United States. *Zootaxa* 3786(2):141-165.

- Trauth, S. E., J. D. Wilhide and A. Holt. 1998. Population structure and movement patterns of alligator snapping turtles (*Macrolemys temminckii*) in northeastern Arkansas. *Chelonian Conservation and Biology* 3(1):64-70.
- van Devender, T. R., and N. T. Tessman. 1975. Late Pleistocene snapping turtles (*Chelydra serpentina*) from southern Nevada. *Copeia* 1975(2):249-253.
- Walker, D., and J. C. Avise. 1998. Principles of phylogeography as illustrated by freshwater and terrestrial turtles in the southeastern United States. *Annual Review of Ecology and Systematics* 29:23-53.
- Walker, D., V. J. Burke, I. Barâk and J. C. Avise. 1995. A comparison of mtDNA restriction sites vs. Control region sequences in a phylogeographic assessment of the musk turtle (*Sternotherus minor*). *Molecular Biology* 4(3):365-374.
- Walker, D., P. E. Moler, K. A. Buhlmann and J. C. Avise. 1998. Phylogeographic uniformity in mitochondrial DNA of the snapping turtle (*Chelydra serpentina*). *Animal Conservation* 1(1):55-60.
- Walker, D., G. Orti and J. C. Avise. 1998. Phylogenetic distinctiveness of a threatened aquatic turtle (*Sternotherus depressus*). *Conservation Biology* 12(3):639-645.
- Whitmore, T. C., and G. T. Prance (editors). 1987. *Biogeography and Quaternary history in tropical America*. Oxford, England: Oxford Science Publications.
- Woodruff, F., and S. M. Savin. 1991. Mid-Miocene isotope stratigraphy in the deep sea: High-resolution correlations, paleoclimatic cycles, and sediment preservation. *Paleoceanography* 6(6):755-806.
- Wright, H. E., J. E. Kutzbach, T. Webb, W. F. Ruddiman, F. A. Street-Perrott and P. J. Bartlein. 1993. *Global climates since the last glacial maximum*. Minneapolis: University of Minnesota Press.
- Wygoda, M. I., and C. M. Chmura. 1990. Effects of shell closure on water loss in the Sonoran mud turtle, *Kinosternon sonoriense*. *The Southwestern Naturalist* 35(2):228-229.
- Yntema, C. L. 1976. Effects of incubation temperatures on sex differentiation in the turtle, *Chelydra serpentina*. *Journal of Morphology* 150(2):453-461.
- . 1978. Incubation times for eggs of the turtle *Chelydra serpentina* (Testudines: Chelydridae) at various temperatures. *Herpetologica* 34(3):274-277.
- Zug, G. R. 1968. Geographical variation in *Rhineura floridana* (Reptilia: Amphisbaenidae). *Bulletin of the Florida State Museum* 12(4): 185-212.

What You Missed at the June Meeting

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(photographs by Dick Buchholz)

On a night with near perfect weather we met in the Peggy Notebaert Nature Museum for what is usually our most popular meeting, our June show and tell session. Having written about this meeting before, it's hard to not repeat myself when describing the members who bring their favorite/most interesting/only reptile or amphibian and talk about the animals that so fascinate us. It's a night that spotlights the diversity that makes up your society. From young to old, new member or old, experienced keeper or novice, we listen to all who are willing to stand in front of the audience and attempt to convey why these animals are so special. And they succeed. Maybe not from being a great speaker or a talented instructor. Maybe not from knowing all there is to know about their animals. Maybe not from having a rare or unique species. They succeed because when they stand up with that particular animal one can feel the connection between person and animal. Even the older, long-time members show a novice-like attachment that is obvious as we sit and listen, hanging on their words, occasionally nodding, sharing the enthusiasm. Of course, that sharing of facts and feelings is what makes the shows that we attend so special. It's exciting to teach the uninformed but interested about reptiles and amphibians. But the June meeting, that's like a mini symposium where we're with people who think as we do. And we empathize. We were that brand new member once. We acquired our first animal at one time. We were surprised by a new fact. I've never seen a bored audience member at the June meeting. Life is a journey, and perhaps the June show and tell is a cross-section of our own journey with herps.

Gail Allinson was first with Mandy, a corn snake that she termed "normal." It certainly looked very much like some wild corns I've come across, with the beautiful reds, blacks, and oranges that rank corns high on the list of beautiful snakes. Gail

learned of the CHS through a lecture and discovered Friends of Scales through our web site. She adopted Mandy through FOS, committing herself to providing Mandy a long and happy "retirement." She obviously has done her homework and with the affection she demonstrated I'm sure that Mandy will live a long and happy life. Kinda nice to have a new member and a common snake start the evening.

Another recent member, Kevin Toberman, brought his little two-year-old Mandarin ratsnake. The snake has the striking colors typical of that species. Kevin said that these snakes tend to eat only live food because they respond to the heartbeats of their prey. The snake he was holding was captive-born from wild-caught parents and had a different personality from his other Mandarin that was several generations from the wild. Unfortunately because they are not aggressive and easily caught these snakes are exploited in Asia for traditional medicines and food.

A little greenish ratsnake appeared next. This is a naturally occurring intergrade between the black ratsnake and the yellow ratsnake. Plucked from a busy road in North Carolina, this snake was presented to Nancy Kloskowski as a gift. She named it Raleigh. The little guy looked fat and happy and is eating well. Then Nancy showed her blacktail cribo, "... although it's not really black. It's dark brown." In the same genus as the indigo, the two-year-old snake showed all the mannerisms of an indigo, actively moving about and using his long tongue and big eyes to explore his surroundings. I suppose because of its Latin American range Nancy named the cribo Red Hot Chili Pepper.



Gail Allinson and her cornsnake, Mandy.



Kevin Toberman with his young Mandarin ratsnake.



Alex Myers brought his Chinese water dragon, Harriet.

Nancy was followed by another long-time member, Dick Buchholz. For two-and-a-half years Dick has cared for a little pancake tortoise he's named Whistle. Dick particularly liked the animal's beautiful shell because when he obtained the animal through our adoptions program, it was covered with a thick layer of mineral deposits. For nine years prior to Dick receiving the tortoise it had been kept in a tub of water. Pancake tortoises are native to some of the dryer parts of Africa and certainly not aquatic. It's amazing that the animal survived, but now it's thriving under Dick's careful attention.

Alex Myers and his lizard showed much aplomb when presenting, probably because he takes the Chinese water dragon to many shows and works with Harriet at home to acclimate her to novel environments and human contact. In spite of her small size, the lizard needs dedicated care. Harriet will soon move into a new cage with plenty of room to climb and swim. Alex says that the animal is very smart and recognizes her name when he calls her.

Joan Moore always has interesting animals from her collection. As she stood with a large (11 lbs.!) ball python draped over her shoulders, she talked about the snake's interesting history. Hatched from a 2003 clutch, the animal, in spite of attempts to feed it, hadn't eaten since last November and normally doesn't eat between November and May. She mentioned that larger snakes tend to eat less. While she knows that the size of that snake is fairly uncommon in captive populations, she wondered whether the wild population might have more of the larger individuals. Possibly breeders mating smaller and younger animals have tended to downsize ball pythons?

One of our younger members, Christian Benz, presented his little Dekay's brownsnake he's had for two years. He feeds it mostly worms, has named it Slither, and knows it's a girl because it birthed 19 babies shortly after he obtained it. Christian said that it was a big surprise when he checked the cage and found these tiny "worms."

Christian's mother Michaelle Benz followed with an Egyptian uromastix. She acquired the lizard from an acquaintance who



Christian Benz spoke about his Dekay's brownsnake, Slither.

did not know the proper care of these lizards. Michaelle said the former owner fed it mostly crickets, and since she's cared for it the very dark colored animal is gradually becoming the lighter color the lizards normally display. She mentioned that the animal now seems to be thriving and active with the proper living conditions, including a plant diet and a 120-degree basking area. Michaelle will even walk the lizard on a leash and says the animal seems to enjoy the attentions of the neighborhood children.

Ben Poldoski brought "Reese's." I'm not positive that he spells the name that way, but it seems appropriate because the coloring of the animal resembles the candy. He showed off his little Kenyan sand boa that he's had for about two years.

Jessica Wadleigh brought two snakes so she could show similarities between two arboreal species from opposite sides of the world. Both were long and slender and strong. The first was a Vietnamese beauty snake with a birth defect that caused a deformity in its spine. The animal was calm for us but Jessica said that it can be defensive if approached rapidly and sometimes bites. It eats well and seems only to be a bit clumsy when climbing because of its deformity. She calls it Chunk. The other snake was a *Spilotes* that has never bitten but will inflate its neck when threatened or aggravated. Both snakes eat rodents but in the wild a large part of their diet would be birds and eggs.

Thus ended our June meeting. I always enjoy the tales of rescues and breeding, care and feeding, but mostly the attention and interest that our members show during this meeting. The diversity of animals is replicated by the diversity of presenters. Bring your favorite/most interesting/only reptile or amphibian next year.

An Ode to Gus

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And when I die, and when I'm gone, there'll be one child born in this world to carry on, . . . to carry on—Blood, Sweat and Tears, Columbia Records, 1969

We're going to go Hollywood with this column. At times, the snakes on our plot demonstrate drama on that sort of scale. We witness sex and violence, interwoven with epic struggles to survive in a land that has barely enough to scratch out a living. Paradise is a nice place to visit, but you wouldn't want to live there. Those that live there have no choice but to make a go of it.

We focus on two snakes with the words that follow. Both are Black-tailed Rattlesnakes (*Crotalus molossus*). One is a male, Cm11, "Gus," and the other is a female, Cm17, "Ms. Gus." The slithering duet have much in common. They're both the same species, occupying the same patches of ground. They consume the same prey items, and seek similar shelters. Both have overcome astronomical odds to survive to adulthood. And they both have exceptionally fat heads. Their fat heads are worthy of mention. Without that crucial tidbit of information, the whole saga that follows is not even worth relaying.

Gus first came the way of the Suizo Mountain Project late in the evening of 17 September 2011. He was found and subsequently captured by John Slone on the north side of Iron Mine Hill. At the time, we had little use for a skinny male *molossus* with a fat head. We'd been there, done that, and had next to nothing to show for it. Hence, he donated some blood, received a PIT tag, and then came the customary unceremonious dump back to his place of capture. He was not even Gus at that point in time. As far as we were concerned, that should have been the end of him.

But then the recapture transpired. On the evening of 3 August 2012, Gus was bagged again. This time, he was found in the wide, sandy wash between Iron Mine Hill and the Suizo Mountains proper. A wave of the PIT tag reader told us who he was. By this point in time, our mission was to put a transmitter into any and all *molossus* that crossed our path. For whatever reason, our surgeon, Dr. Dale DeNardo, took a shine to this slender and fat-headed snake. He felt compelled to name this snake after his fat-headed dog, Gus. Naming a fat-headed snake after a fat-headed dog is, in short, brilliant! Hence, the name stuck. Soon after, Gus was in the game, performing great deeds of Gus-dom. For a scrawny, fat-headed snake, he really got around!

On 16 September 2012, Marty Feldner led the field class of Wolfgang Wüster on a Roger-less outing. Gus was now wired, and whatever student was in charge of the antenna tracked him down. Gus was discovered paired with a female—the future Ms. Gus. The first glimpse of Ms. Gus inspired Marty to comment: "Yegads! Her head is even fatter than his!" (Figure 1). At that point in time, we were out of transmitters. Ms. Gus was left alone that night. As soon as I got wind of the pairing, a rush

order for a new transmitter was placed. And the directive was that until we got the transmitter, we were to leave the pair alone. If we were ever to observe reproduction of the species on our plot, mating had to ensue.

My first visual of the pair was on the evening of 28 September. They were in a miserable snarl of a packrat midden that was packed into the root system of a particularly sinister and sprawling catclaw acacia. The thorny hell hole was nicely accentuated by a ring of chest-high prickly pear, which all but blocked the view in. Much blood was lost in trying to get a visual of Ms. Gus. When I finally did see her, I also was inspired to say: "Yegads! Marty is right! Her head *is* fatter than his!"

The game of cat and mouse between the fat-headed snakes and their fat-headed trackers continued on into October. The whole experience was a three-week-long festival of fatheads. On the evening of 5 October, Marty and I had split the tracking duties, and Marty had Gus on his route. At 8:09 P.M., Marty summed up what he saw by flatly writing on the datasheet: "It is good night to fornicate!" (He didn't actually write "fornicate." He instead utilized the Holy Grail of foul language, the foo foo word. That's right—he cussed on a datasheet, and we got *that* in writing.)

Despite the rather abrasive start to the words Marty scrawled on the page that night, the rest of the description is as fluid and smooth as the action he witnessed: "Cm11 is in coitus with a female (equivalent to his size and maybe heavier) at the edge of a staghorn cholla midden constructed in prickly pear. When first seen, Cm11 was head jerking and chin rubbing along flank of unknown female. He continued this behavior on and off for 8-10 minutes until female moved to investigate me. This is when the tails became exposed and I could see for certain that they were locked up. Female dragged him by his wang so they were stretched out in opposite directions, weaved through the prickly pear over the next few minutes. Cm11 worked his way back to female and resumed chin rubbing flanks and dorsum, taking breaks periodically to lie motionless and enjoy contemplating



Figure 1. 16 September 2012: First look at the pairing of Gus and Ms. Gus. "Yegads! Her head is even fatter than his!" Refer to text for details. Image by Martin J. Feldner



Figure 2. 5 October 2012: The pairing continues for nearly three weeks. Here we see Gus wooing Ms. Gus. Image by Martin J. Feldner

which hemipene he was using. Tongue flicking accompanying most chin-rubbing motions.” (Figures 2 and 3).

Did you guys catch some of these words?

“Female dragged him by his wang? Taking breaks to contemplate which hemipene [sic: hemipenis] he was using?” How you talk, Feldner! But just in case, that would be the right hemipenis, Gus. Did Gus know his right from his left? I’ll bet he did on this night! All joking aside, Marty’s write-up of this incident was pure artistry. Working at night with nothing but a headlamp, a clipboard, a pen, a vivid imagination, and a blank page to fill is an arduous process. And the lure of what comes next is always strong with many interesting serpents on the list to track. To his credit, he stayed with it.

Speaking of staying with it—so did Gus! The next morning, Mr. Feldner and I did not let any grass grow under our feet getting back to the spot where the action was transpiring. We arrived at 7:55 A.M. to see that the pair was still “locked up.” This is where our scruples might very well have been in the way of gaining a new study animal. My rules for capture of a new snake do not allow for breaking up a couple that is f-f-f-fu, er uh, foo, forn—uh—in coitus. Coitus! Yeah—that’s the acceptable scientific term for it. What a boring (literally *and* figuratively) word “coitus” is. As the images plainly demonstrate, Gus had her stuffed like a Christmas goose. He was so into her that we heard bones popping. (Coitus, indeed. Wow, what a geyser of terminology . . .) We were prepared for a long wait. They had already been coitusing for 12 hours, and could easily go another 12 before it was over.

But suddenly, Ms. Gus did us the ultimate favor. Upon seeing us looming large above her, she panicked, and began sprawling pell-mell toward the entrance to the (Packrat) midden that Marty had described the night previous. Poor Gus was still in her, so to speak, and was haplessly wrapped like an anchor line about the prickly pear. Ms. Gus began a series of jerking motions, (yehaw!), trying to get free, but she only gained an inch or so. (Gus’s “wang” also likely gained an inch or so in the process). With a powerful surge, Ms. Gus broke free, literally hanging Gus out to dry in the process. With Ms. Gus now unconnected, Roger’s rules for breaking up a couple no longer



Figure 3. 5 October 2012: Coitus! Image by Martin J. Feldner

applied. She was snagged and bagged, and female Cm17 was now in the game! That’s the end of that story—and the beginning of the next.

We of course had to take Ms. Gus home with us for a couple days, in order to line up and perform a surgery. This left our hapless hero Gus to smoke his after-sex cigarette alone, and maybe get “righty” back into its proper moorings. After that, he was off to the races. The pencil necks had just snatched his coitus buddy. There was no sense in his hanging out while waiting to ascertain what would come of *that* flandickery. He bombed across Suizo Wash, and made a major shift along the southern flank of the Suizo Mountains. While there were occasional signs of settling in at a couple places, he never actually hibernated. He stayed on the go throughout the winter, and eventually had moved further north and east than any other animal on our plot. The skinny fathead was a machine!

By the time we got Ms. Gus back to her capture spot, Gus was long gone. While it is unlikely that she was pining for her man, she remained at her capture site for what seemed like two forevers (Figure 4). Finally, by 4 November, she had jetted across the wash, and was near the top of the extensive southwest ridge of the Suizo Mountains proper. She eventually went over



Figure 4. 27 October 2012: Ms. Gus has now been thoroughly processed, and has had a transmitter surgically implanted. She remains at her capture site for nearly a month before finally moving on. Image by the author.



Figure 5. Ms. Gus finally begins major movements to the north, and by 8 December 2012, enters what will not only be her overwintering site, but also her chosen parturition site. Image by the author.

top, and dropped into the lower bowels of Tim Canyon. She was viewed surface-active until 4 December. She was very thick in girth at that point. With the next tracking session, 8 December, she had slipped into an impressive and extensive west-facing boulder structure. It was here that she overwintered, and was not seen again until 11 March 2013.

The author of this epic column decided that a thorough description of the overwintering site of Ms. Gus is in order. This is not because your author is so fond of typing that he wants to aimlessly go about whittling his fingers to the second knuckle describing a rock pile with a cold snake in it. (Although that is certainly reason enough for the effort). No, this hibernaculum was to play a big role in what follows.

Two paragraphs ago, mention was made of a place called Tim Canyon. This canyon is the southernmost of three different slot canyons that drain the western side of the Suizo Mountains. As one approaches the canyon from the west, it rumbles gently upward in eastward fashion for a distance of about 300 meters. The canyon then bends abruptly, steepens in aspect, and heads upward and northward as one continues the ascent. It eventually



Figure 7. 6 January 2013: Gus viewed out basking in the dead of winter. His propensity for remaining active and visible throughout the winter of 2012–2013 made him a favored tracking target. Image by Martin J. Feldner.



Figure 6. From the “porch” of Ms. Gus, looking down Tim Canyon. To get to this site, she has traveled over 700 meters. She crawled over top of the ridge viewed left-center, traveling from Iron Mine Hill, which is behind everything to the left of the photo. Image by the author.

peters out, and becomes the steep, south facing flank of the third highest point in the Suizos.

Ms. Gus chose to den at the point where Tim Canyon makes the bend. She was 30% up the east flank of the adjacent slope. The due-west-facing granitic bedrock structure that she selected is roughly three meters tall and nearly perpendicular to the slope, by perhaps three meters wide (the width is actually bedrock welded into the hillside), and roughly 40 meters long south-to-north. The base of this structure has all manner of entranceways, from cavernous openings to tight crevices. There were 50 ways to leave her cover. Lush vegetation grows just west of the bottom of this structure. In short, it was a good place for a fat-headed *molossus* to be (Figures 5 and 6).

While Ms. Gus remained buried in her over-wintering site, her man remained constantly on the move. He was observed basking and surface-active throughout the winter. When radio-tracking our subjects in the dead of winter, we always considered it a major coup of sorts to get any kind of visual. With Gus, there was always a high probability of not only obtaining a visual, but also getting some good images of a rattlesnake fully basking outside its shelter (Figure 7). With Ms. Gus, all tracking sessions were a matter of standing outside her outcrop writing up nothing. Conversely, when we tracked Gus, we made sure we did it together, for we always knew we were in for a treat at the end of the tracking experience. And while Ms. Gus continued her act as the invisible woman, by early March, Gus was already steadily churning his way back to Iron Mine Hill.

Finally, on 11 March, Ms. Gus began showing herself. But her egress from the site was slow and methodical. It was not until 29 March that she finally began easing away, and an image taken by Marty reveals a snake with some hefty distal plumpness (Figure 8).

Upon emerging from her overwintering site, Ms. Gus made a series of mini moves that at first led us to believe that she was going to leave Tim Canyon. She seemed to be backtracking her autumnal movements. But once she got to near the top of the southwestern ridge of the Suizos proper, she began to slip back down again. By 29 June, she was back at her overwintering site.



Figure 8. 29 March 2013: Just after leaving her overwintering site, Ms. Gus already shows signs of her pregnancy. Image by Martin J. Feldner.

Marty was able to get two visuals of her basking in July. With each of these visuals, he commented on how thick she had become toward the rear.

I did not see her again until 3 August. On this day, Jerry Schudda and Rick Bowers were assisting me with tracking duties. It was hot, and we were ready to quit. When I suggested that we had a pregnant female *molossus* we could check, they were gung ho—despite the distance of the hike in the searing heat. Their willingness to do this was commendable. As a result, I was not only able to get a visual, but found that she had moved about 30 meters northward, along the lower edge of her structure. She was discovered coiled under a boulder overhang at the northernmost reach of the structure. I had time to squeeze off one photo of her coiled in situ. Then she bolted into a hole that was just behind her. I squeezed off two more shots of her hefty rear flank before she could slip out of sight (Figure 9). She was, without question, a very pregnant *molossus*. And this was to be the last time we saw her pregnant.

By 7 August, she had made a ping-pong move back to her hibernaculum. She was not visible, as usual. Two days later, the ever lucky Marty Feldner discovered a male neonate *molossus* out crawling on top of one of the boulder stacks, less than two meters from where she had overwintered. In short, her hiberna-



Figure 9. 3 August 2013: Still pregnant! Image by the author.

culum was the same place as her parturition site! While this is a common occurrence with many species of rattlesnakes at higher elevations, it was an absolute first for us. Out of 12.5 years of observing rattlesnake parturition over 40 times, in three species of rattlesnake, this was the one and only time that this happened.

Marty and I had not discussed what to do if we encountered any neonates. Hence, on 9 August, he made the executive decision to collect the one he saw. His rationale was one of getting DNA from the little fella. There was no hot surge of joy when, on the morning of 10 August, Marty showed me his little prize. I was of course stoked that we had our first birthing incident with *molossus*, but I had these dreams of seeing piles of babies hanging out with mommy. If we went wading in and removing them as we found them, no such thing could ever happen.

Marty was off to other lands in the week that followed. This left me with the nest site of Ms. Gus all to myself. (What a pity.) There would be no more of this taking babies from mamma! Needless to say, I hit that rascal morning and night for the next week to follow. I became the invisible man at work and at home. I'd go out and stay out until midnight, get up the following morning at 4 A.M. and hit it again. While I was doing that, reports and images came trickling in from other parts of the country. In all, three other groups had nesting *molossus*, and all

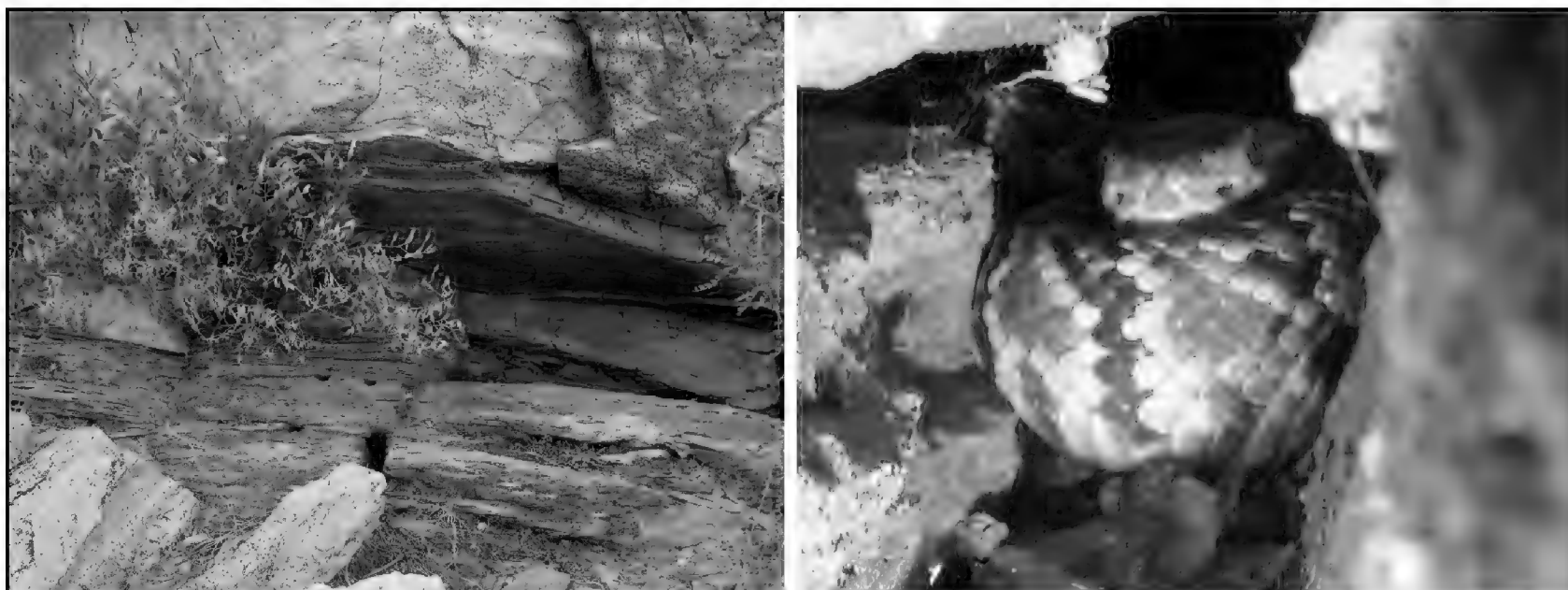


Figure 10. 12 August 2013: This was to be the only neonate found by the author at the parturition site of Ms. Gus. (Left) Lower center, the outside view of the crevice in which the neonate was found. (Right) The extremely difficult-to-get image of the youngster in situ. Note that this neonate still retains the prebutton, indicating that it has not yet shed. Images by the author.

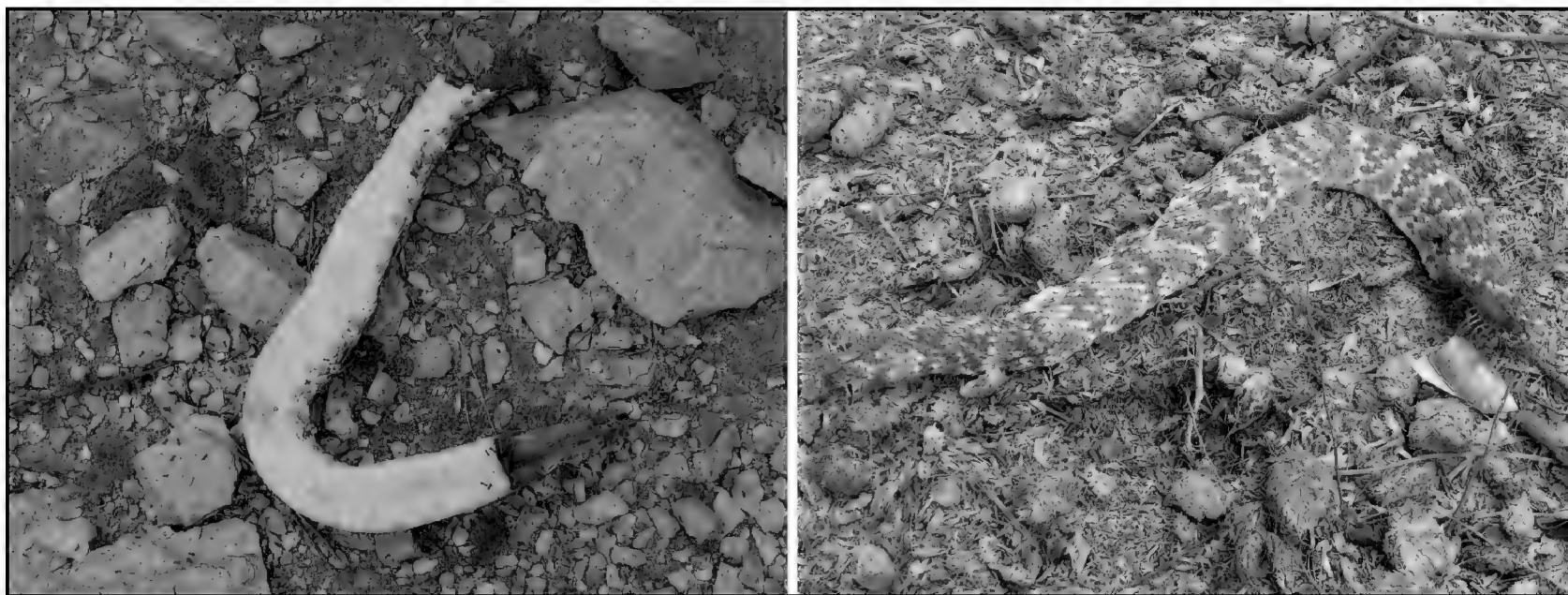


Figure 11. 22 September 2013: While likely en route to visit Ms. Gus, some one or some thing got him. Gus, you are not forgotten, and you will always be in our hearts. Images by the author.

three got great images of mothers with babies. That's right, I had these *kids* upstaging me! I had invested thousands of dollars and hours to set myself up for moments such as this, while others lounged about scoring without breaking a sweat. I was walking a mile, twice a day, to attempt to get what they had going on at their back porch. This would have been acceptable if only I got some of the action that should have been my reward.

Nope, when all was said and done, on 12 August, I found one neonate *molossus* that I had no business finding at all. It was found in a narrow vertical crevice just outside what was determined to be the preferred entrance hole to the nest. (Figure 10). Back home, the neonate that Marty had collected shed his skin on 14 August. That evening, I processed him. He was released at the nest site on 15 August. By 16 August, Ms. Gus had cleared out of her nest site, and her birthing experience was behind us. There were to be no cool images of mom and babies hanging out together. No neonate shed skins were found in or around the nest site. While it could have all been worse, despite all the effort, our first *molossus* birthing experience was a rather lackluster affair. We had a fat snake that morphed into a skinny snake, and two neonates that proved the nesting experience had actually happened.

We did not track Ms. Gus again until 24 August. By this time, she had crawled out of the bowels of Tim Canyon, had gone over the top of the southern ridge of the Suizo Mountains, and was hanging around a wash just east of Iron Mine Hill. It was this wash that Marty first photographed her and Gus together (Figure 1). Once she was in this vicinity, I knew it would only be a matter of time before Gus found her. We ramped up our efforts on these two animals accordingly. For nearly a month, Gus showed no interest in tracking his lady down. But on the evening of 20 September, the pair was viewed less than fifty meters apart. Gus seemed poised to go courting again.

The morning of 22 September found Gordon Schuett, Ryan Sawby, and me close to where Gus had been tracked a day-and-a-half previous. Upon raising the antenna skyward, it was noted that his signal was leading us directly toward where Ms. Gus had last been seen. He seemed to be heading straight for his lady. The flag hung 36 hours earlier for Ms. Gus waved in the breeze, just 30 meters to the south. Reunited? Hot diggity damn! Anticipation caused me to ignore the signal, and head for the

flag. It was then that it all came to an abrupt end.

"Wait a minute, Roger!" Gordon sounded off from behind me. "Is this what we're tracking?" As he made the inquiry, he deftly hooked a section of snake flank from out of a prickly pear. It was Gus, or rather, what was left of him. The 600 mm of flank that Gordon had flipped out of the prickly pear was now upside down, on open, rocky bajada. Hence, my first glimpse was of the white belly scales facing up. Both ends of Gus's midsection showed the jagged signs of biting, tearing and ripping on the part of some unknown predator. Moderate-size black ants were working both ends of the severed corpse. There was no head or tail to be found in the vicinity, just the hefty mid flank, which still contained the transmitter. What remained was fresh, there was no stench, and the ants had barely begun the cleanup process. Gus had not been dead long (Figure 11).

Next came the photographs, the gut-wrenching mortality write-up, and the wild speculation as to how this had happened. Gordon and Ryan heavily favored human predation. My own theory was that this was a natural event. My personal guess is that it was the work of a coyote. As we don't really know for certain what got him, there is no need to belabor the point. What we do know is that a very favored subject of ours was no longer with us. We had grown quite attached to our skinny, fat-headed and randy *molossus*. What made it all the more painful was the fact that Gus was cut down just as he was zeroing in on his lady. We had high hopes of picking off yet another annual pairing within the species. (We stop short of claiming monogamy with *Crotalus molossus*, but have gathered evidence of the same couples getting together year after year).

Meanwhile, in a hallowed drawer of my refrigerator, stowed in a sealed plastic bag is a shed skin of a neonate male *molossus*. Sealed within that bag is a notecard that refers anybody interested to page 19 of the DNA section of the official three-ringed binder of the Suizo Mountain Project for 2013. Page 19 contains all the vitals on this snake. And what the scribe did not capture with words, the camera did. We have nailed this lad nine ways to Sunday. Is this the son of Gus? This author thinks so! We certainly have the proof, one way or the other. We witnessed the paring, we photographed the mating, and we stuck with the pair for a full year. The field observations that back our little sample almost make it all a forgone conclusion. I'd bet any amount of

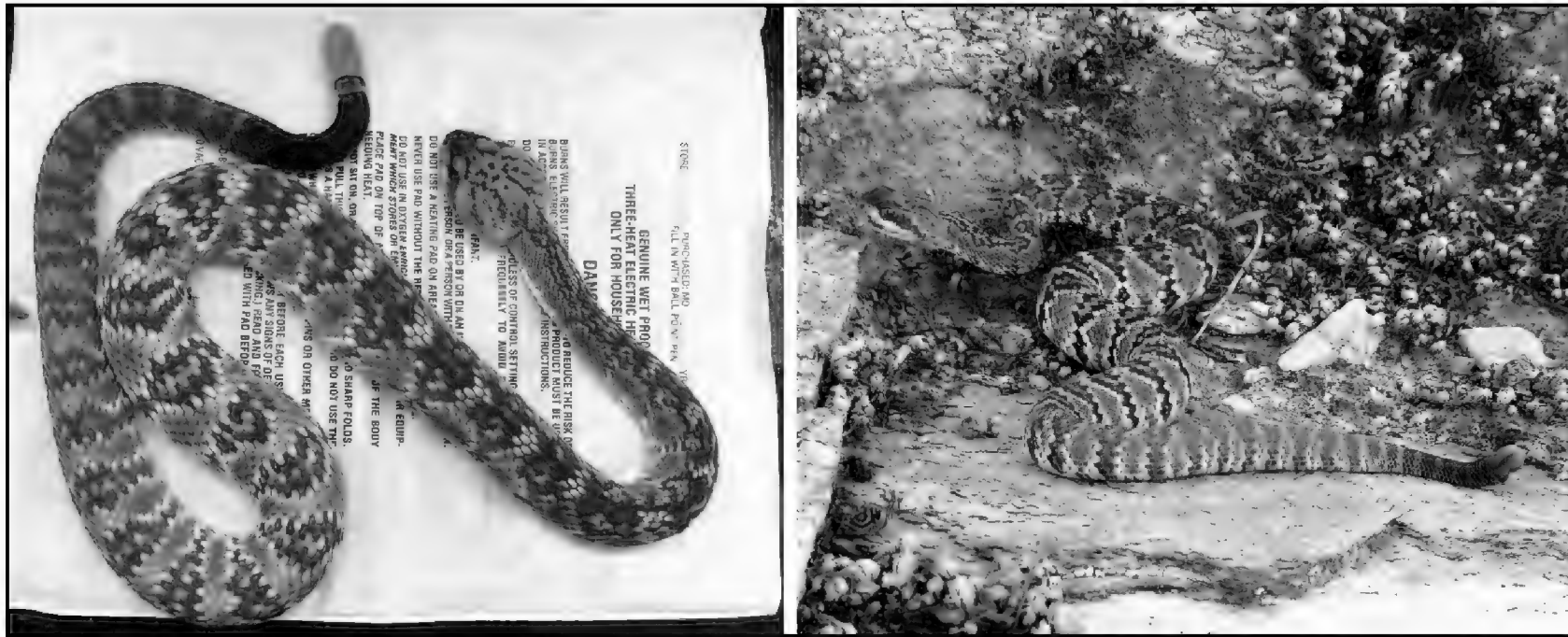


Figure 12. Father and son? This author thinks so! We'd like to think that Gus Jr. followed in his father's footsteps. In my own perfect world, that would happen! Images by the author.

money that this is indeed the son of Gus. Will he "carry on?" Not without a lot of blood, sweat and tears! Though the odds are against him, this author sincerely hopes that he does (Figure 12).

This here is Roger Repp, signing off from Southern Arizona, where the turtles are strong, the snakes are handsome, and the lizards are all above average.

Minutes of the CHS Board Meeting, April 15, 2016

President John Belah called the meeting to order at 7:40 P.M.
Board members Brandon Ottolino and Mike Scott were absent.

Officers' Reports

Recording secretary: Teresa Savino read the minutes of the March board meeting, which were corrected for typos and accepted.

Treasurer: Amy Sullivan read the financial report.

Vice-president: Jessica Wadleigh listed the upcoming speakers.

Corresponding secretary: Amy Bochenko

Membership secretary: Mike Dloogatch read the list of memberships that had expired.

Sergeant-at-arms: Brandon Ottolino was not present. Attendance at the March meeting was 35.

Committee Reports

Shows:

- Notebaert Nature Museum, first full weekend of each month. The list of upcoming shows was reviewed. Dick Buchholz will be covering most. Will need people for the June Notebaert show because Dick will be out of town. Many people attended the Family Pet Expo at Arlington Race Track

Adoptions: At ReptileFest 18 animals were adopted out

Junior herpers: Attendance was 40 at the April meeting, at which the topic was reptile reproduction. May meeting is on Mother's Day. Will show a movie. Kids helped at ReptileFest.

Everything went well. A field trip is tentatively scheduled for May 23, site to be determined.

Library: Mike Dloogatch brought new edition of the *Peterson Field Guide to Reptiles and Amphibians of Eastern and Central North America*. Suggested getting 2 copies for the Library. Teresa suggested getting some up-to-date DVDs. Asked for suggestions.

Old Business

ReptileFest: Nicky Copeland, who has been coordinating the advertising for 'Fest for the last 5 years, gave a report. Every local TV station brought a camera to 'Fest. NBC did a live stream on Sunday. There were ads on Facebook. Andy reported attendance was 7519. The CHS had to get a permit this year from the city of Chicago. This will be an ongoing requirement.

New Business

Dick got a letter from Gilbert Neil from the Garfield Park Conservatory. He is thinking of getting geckoes and toads to help control pests. He is looking for some advice. Aaron LaForge will contact him.

John Archer suggested making radio personality Steve Dale a permanent member. He has been providing help and coverage for a number of years. This was approved.

The meeting adjourned at 9:37 P.M.

Respectfully submitted by recording secretary Teresa Savino

Herpetology 2016

In this column the editorial staff presents short abstracts of herpetological articles we have found of interest. This is not an attempt to summarize all of the research papers being published; it is an attempt to increase the reader's awareness of what herpetologists have been doing and publishing. The editor assumes full responsibility for any errors or misleading statements.

BIG MOUTH CAVE SALAMANDERS

M. L. Niemiller et al. [2016, Copeia 104(1):35-41] note that salamander species that live entirely in subterranean habitats have evolved adaptations that allow them to cope with perpetual darkness and limited energy resources. They conducted a 26-month mark-recapture study to better understand the individual growth and demography of a population of the Big Mouth Cave salamander (*Gyrinophilus palleucus necturoides*). They used a growth model to estimate growth rates, age at sexual maturity, and longevity, and an open population model to estimate population size, density, detectability, and survival rates. Furthermore, they examined cover use and evidence of potential predation. Individuals probably reach sexual maturity in 3–5 years and live at least nine years. Survival rates were generally high (>75%) but declined during the study. More than 30% of captured salamanders had regenerating tails or tail damage, which presumably represent predation attempts by conspecifics or crayfishes. Most salamanders (>90%) were found under cover (e.g., rocks, trash, decaying plant material). Based on 11 surveys during the study, population size estimates ranged from 21 to 104 individuals in the ca. 710 m² study area. Previous surveys indicated that this population experienced a significant decline from the early 1970s through the 1990s, perhaps related to silvicultural and agricultural practices. However, the results of this study suggest that this population has either recovered or stabilized during the past 20 years. Differences in relative abundance between early surveys and this survey could be associated with differences in survey methods or sampling conditions rather than an increase in population size. Regardless, this study demonstrates that this population is larger than previously thought and is in no immediate risk of extirpation, though it does appear to exhibit higher rates of predation than expected for a species believed to be an apex predator of subterranean food webs.

INTRODUCED ALPINE NEWTS

J. W. Arntzen et al. [2016, The Herpetological Journal 26(1): 49-56] note that the last century has seen an unparalleled movement of species around the planet as a direct result of human activity, which has been a major contributor to the biodiversity crisis. Amphibians represent a particularly vulnerable group, exacerbated by the devastating effects of chytrid fungi. The authors report the malicious translocation and establishment of the alpine newt (*Ichthyosaura alpestris*) to its virtual antipode in North Island of New Zealand. They use network analysis of mitochondrial DNA haplotypes to identify the original source population as *I. a. apuana* from Tuscany, Italy. Additionally, a population in southern France, presumed to be introduced, is identified as *I. a. alpestris* from western Europe. However, the presence of two differentiated haplotypes suggests a mixed origin. This type of analysis is made possible by the recent availability of a phylogenetic analysis of the species throughout its natural range. The particulars of both introductions are discussed.

WIDESPREAD HYBRIDIZATION BETWEEN TWO SPECIES

R. M. Lehtinen et al. [2016, Copeia 104(1):132-139] note that since the advent of molecular tools, hybridization has increasingly been recognized as both a common and an evolutionarily important process. Using single nucleotide polymorphism markers from three nuclear genes, they investigated the extent of hybridization between two terrestrial salamanders (*Plethodon cinereus* and *P. electromorphus*) at 13 sites in northeastern Ohio. These markers indicated a high degree of gene flow and introgression in these two species (48 of 90 individuals genotyped were classified as hybrids). These hybrids included F₁ individuals and backcrosses to both species. These data as well as mitochondrial DNA sequences from hybrids suggest symmetrical hybridization. A multivariate analysis of standard morphological characters and coloration patterns from image analysis demonstrated that hybrids are intermediate in many ways. However, backcrosses proved difficult to separate from parentals, and the extent of hybridization would have been underestimated using morphology and coloration alone. Given the high frequency of hybrids and their broad geographic distribution, the authors speculate that these two lineages may be in the process of merging back into a single gene pool.

MIDWINTER EMERGENCE

E. J. Nordberg and V. A. Cobb [2016, Journal of Herpetology 50(2):203-208] note that hibernation is an important behavioral event in temperate-region reptiles for escaping periods of harsh winter temperatures. Generally considered a dormant period, observations of winter activity suggest that hibernating reptiles may be more active than initially thought. To examine winter activity in a species that commonly hibernates, timber rattlesnakes (*Crotalus horridus*), the authors monitored the detailed movements and body temperatures (T_bs) of free-ranging snakes over two winters. Hourly T_bs and movements of snakes throughout a five-month hibernation period were monitored for midwinter activity and potential thermoregulatory behavior. Environmental temperatures and snake operative temperatures were used to estimate time periods when snakes were at or on the surface. Visual observations of snakes basking on the surface were uncommon; however, hourly recorded snake T_bs revealed that 69% of the snakes emerged to the surface to bask two or more times for a total of 60 emergence events from 14 individuals. Snake T_bs (N = 53,041) during hibernation were 11.1 ± 3.5°C (mean ± SD) and ranged from 1.1–33.7°C. Counter to prediction, calculated estimates of metabolic expenditure associated with increasing T_b (via basking or surface emergence) during hibernation had little effect on the total energy budget required to survive winter. Additional metabolic expenditure attributable to multiple basking events (e.g., 10 basking events) can be offset by acquiring as little as 1.0 g of rodent during the active season.

NILE CROCODILES IN SOUTH FLORIDA

M. R. Rochford et al. [2016, Herpetological Conservation and Biology 11(1):80-89] report that the state of Florida has more introduced herpetofauna than any other governmental region on Earth. Four species of nonnative crocodilians have been introduced to Florida (all since 1960), one of which is established. Between 2000 and 2014 the authors field-collected three nonnative crocodilians in Miami-Dade County, Florida, and one in Hendry County, Florida. DNA barcoding and molecular phylogenetics were used to determine species identification and native range origin. Also, diet, movement and growth were described for one crocodile. The molecular analyses illustrated that two of the crocodiles collected are most closely related to Nile Crocodiles (*Crocodylus niloticus*) from South Africa, suggesting this region as a source population. This documented the first known introduction of *C. niloticus* in Florida. Two, and possibly three of the introduced crocodiles shared the same haplotype, suggesting they are likely from the same introduction pathway or source. One animal was captured, measured, marked, and released, then recaptured 2 y later allowing the authors to calculate growth rate (40.5 cm/y) and movement. The most likely route of travel by waterway (i.e., canal) illustrates that this animal traveled at least 29 km from its original capture site. One crocodile escaped from a facility in Hendry County, Florida, and survived in 1,012 ha of semi-wild habitat for three to four years, confirming that this species can survive in southern Florida.

LONG-TERM STUDY OF A SNAKE COMMUNITY

C. H. Ernst et al. [2016, The Herpetological Bulletin 135:15-23] studied the population characteristics of a community consisting of 16 species of snakes occurring in five microhabitats for 24 years (1982 to 2006) at the Mason Neck National Wildlife Refuge, Fairfax County, Virginia. The portion of the refuge studied included five varied microhabitats: an old farmstead, and old field, extensive woodlands, a pond, and a tidal marsh. The species morphological characteristics, adult male/female ratios, and juvenile/adult ratios are reported, as also are the snake biomass, numbers, richness of each microhabitat and changes in the fauna over the time period. Niche characteristics of the snake species are described. Comparisons are made with Middle Atlantic snake communities to the north and south of Mason Neck.

SEMITERRESTRIAL TADPOLE

C. H. L. Nunes-de-Almeida et al. [2016, Journal of Herpetology 50(2):289-294] note that frogs in the genus *Cycloramphus* are endemic to the Brazilian Atlantic Forest domain and many are threatened or endangered. *Cycloramphus* species lay eggs either on moist rocks or in moist soil cavities on the ground. Tadpoles of only 8 of the 28 recognized *Cycloramphus* species are known. The authors describe the tadpole of *C. rhyakonastes* on the basis of specimens collected at the type locality in southern Brazil. *Cycloramphus rhyakonastes* is an aquatic breeder with semiterrestrial tadpoles that live on moist rocks within the splash zone of high gradient streams. The authors compare the *C. rhyakonastes* tadpole with all congeneric tadpoles described to date and discuss adaptations in this specialized tadpole and those of other species that adhere to rocky substrates.

RING SPECIES

S. R. Kuchta and D. B. Wake [2016, Copeia 104(1):189-201] note that ring species are widely recognized as one of the best natural illustrations of species formation. A ring species is a circular arrangement of populations with one boundary characterized by reproductive isolation, but intergradation among populations elsewhere. They form when populations disperse around a central barrier and form a secondary contact characterized by reproductive isolation. Ring species are often presented as a taxonomic conundrum, because the presence of a single boundary exhibiting reproductive isolation leaves the ring of populations uncomfortably situated between one and two species. The authors review the ring species concept, with a focus on the salamander *Ensatina eschscholtzii* and the greenish warbler, *Phylloscopus trochiloides*. They argue that ring species demonstrate the gradual nature of species formation, and thereby illustrate the model of species formation originally put forth by Darwin. They also argue that ring species have become overly idealized, with a focus on strict criteria to the detriment of evolutionary lessons. Like all models of evolutionary change, the ring species concept is an oversimplification, and an ideal ring species has never been found. Finally, they review ring species in light of the general lineage concept of species, and argue that ring species status, while nicely accommodated by recognizing a single species, is independent of taxonomy. The essential features of a ring species are a biogeographic history resulting in a ring-like distribution, and the presence of a single species border characterized by reproductive isolation. Under the general lineage concept, reproductive isolation is a contingent, but not necessary, property of evolutionary lineages. Whether one considers a ring species complex to be one species or many does not change the evolutionary message, and the problems (and lessons) presented by ring species do not go away with taxonomic changes.

A REVIEW OF HEARING IN PLETHODONTIDS

G. Capshaw and D. Soares [2016, Copeia 104(1):157-164] note that the ability to detect airborne sound using a pressure-transducing tympanic ear has evolved several times over the course of vertebrate history, suggesting that hearing is an advantageous modality and an informative model for sensory evolution. Amphibian hearing is especially interesting because these animals must negotiate water to land transitions. Salamanders are good animal models for the study of hearing, not only because they have a wide range of ear morphologies, but also because they have evolved extratympanic pathways for sound and vibration transmission. The authors suggest that sufficient extratympanic hearing in salamanders and reduced reliance on vocal communication has relaxed selection on the auditory system and allowed for the structural diversity of the salamander ear. Unique among salamanders is the family Plethodontidae, which is not only the most speciose and ecologically diverse family of salamanders, but also possesses a highly derived ear with great inter-specific variation. This review provides an overview of historical and current research on acoustic behavior, auditory anatomy, evolution, and physiology, and highlights plethodontid salamanders as an informative model for study of extratympanic function and auditory evolution.

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UPCOMING MEETINGS

The next meeting of the Chicago Herpetological Society will be held at 7:30 P.M., Wednesday, July 27, at the Peggy Notebaert Nature Museum, Cannon Drive and Fullerton Parkway, in Chicago. This meeting will feature **Douglas R. Mader, D.V.M.** Dr. Mader, co-owner of the Marathon Veterinary Hospital in the Florida Keys, will speak about “Iguanas in the Florida Keys.” The green iguana (*Iguana iguana*) has been one of the most popular reptile pets ever in the United States—except for the Florida Keys. Green iguanas are common in the tropical island chain and are considered pests by locals. So much so that there is a bounty on the reptiles and an “open season” on them. It is legal to shoot and kill iguanas providing that they are killed with a single shot. This talk will discuss the ecological impact of the popular pet, the origin of the problem and possible solutions.

Ted Levin, author of *America’s Snake: The Rise and Fall of the Timber Rattlesnake*, will speak at the August 31 meeting. Ted has worked as a zoologist at the Bronx Zoo, a naturalist for the National Park Service, and a wildlife biologist for the Audubon Society. He is the author of *Blood Brook: A Naturalist’s Home Ground*, *Backtracking: The Way of the Naturalist*, and *Liquid Land: A Journey through the Everglades*, which won the Burroughs Medal for exemplary nature writing in 2004.

The regular monthly meetings of the Chicago Herpetological Society take place at Chicago’s newest museum—the **Peggy Notebaert Nature Museum**. This beautiful building is at Fullerton Parkway and Cannon Drive, directly across Fullerton from the Lincoln Park Zoo. Meetings are held the last Wednesday of each month, from 7:30 P.M. through 9:30 P.M. Parking is free on Cannon Drive. A plethora of CTA buses stop nearby.

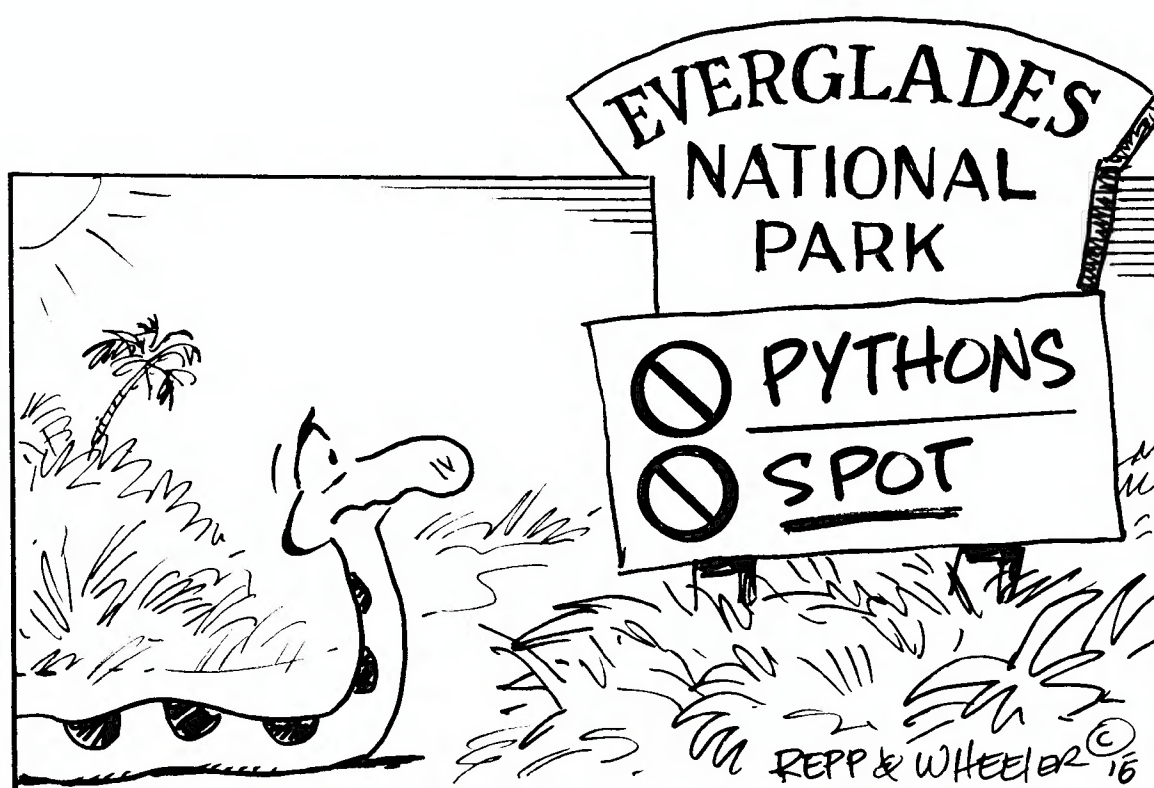
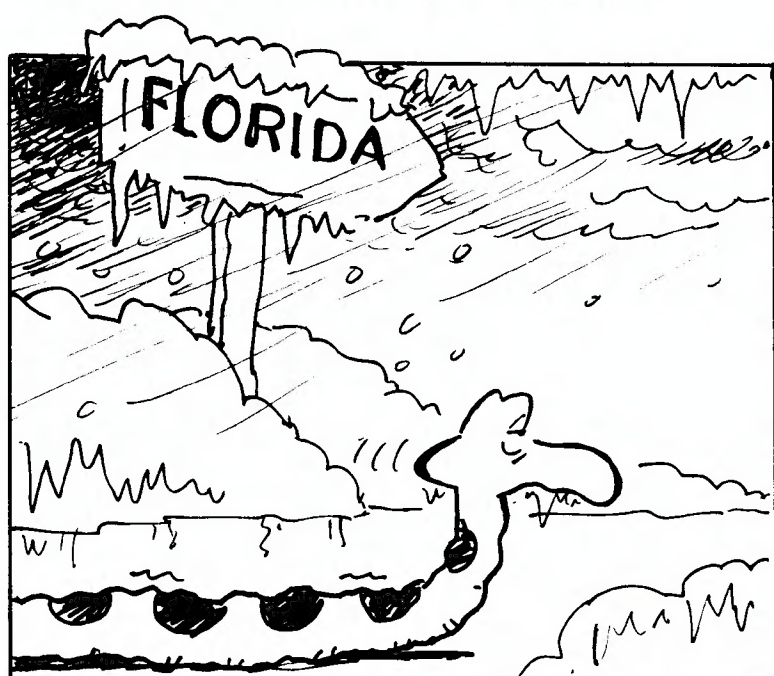
Board of Directors Meeting

Are you interested in how the decisions are made that determine how the Chicago Herpetological Society runs? And would you like to have input into those decisions? If so, mark your calendar for the next board meeting, to be held at 7:30 P.M., Friday, August 19, 2016, at the Schaumburg Township District Library, 130 S. Roselle Road, Schaumburg.

The Chicago Turtle Club

The monthly meetings of the Chicago Turtle Club are informal; questions, children and animals are welcome. Meetings normally take place at the North Park Village Nature Center, 5801 N. Pulaski, in Chicago. Parking is free. For more info visit the group’s Facebook page.

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